THE BRITISH LOWER JURASSIC SPECIES OF THE BIVALVE GENUS *CARDINIA*

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CONTENTS

SUMMARY

Seven new species of *Cardinia* are described and sixteen others recognized in the British Lias. These are grouped under four informal, infra-generic groups: Deltoids, Ovoids, Concinnoids and Rugoids. The new species are *subabducta, raasayi, huntcliffensis, subobovata, tuffleyensis, dayi* and *tutcheri*. A list of the specific names available in the genus *Cardinia* is included. Neotypes of *Cardinia crassiuscula* (J. Sowerby) and *C. laevis* (Young & Bird) are designated. The hinge notation of *Cardinia* is discussed and shown to have been wrongly interpreted by previous workers. Discussion of the palaeoecology and evolution leads to the conclusion that the

characteristic hinge of *Cardinia* was persistent throughout the range of the genus and that it was a strong mechanism for resisting shear action. This is taken to indicate that these bivalves were active shallow burrowers. Arguments are offered which suggest that the generic relations of *Cardinia* are with the Lucinacae rather than with the Crassatellacae, and that oxygen availability was the principal limiting factor controlling their distribution.

I. INTRODUCTION

THE NUMBER of species described under, or subsequently referred to, the genus *Cardinia* exceeds 120. This large and variable group of heterodont bivalves would, if it were living, cause no little concern to the neontologists – even with the living animal to assist in classification. Palaeontologists, with nothing but shell morphology to work on, demonstrate their perplexities in the extremes to which their systematic philosophies lead them.

Brauns, in 1871, with some 43 named forms to classify, placed them all in synonymy with J. Sowerby's three 'classic' species – *Cardinia concinna, C. crassiuscula* and *C. listeri.* On the other hand Hayami (1958) listed 111 names and recognized 75 of these as true species of *Cardinia.*

At the generic level five names were proposed for the group before Cox (1951) stabilized the genus *Cardinia* to date from Agassiz, 1841. Hayami grouped his 75 species into six unnamed subgeneric groups. For general purposes the majority of *Cardinia* species fall into four groups, three of which correspond with Brauns' three 'species'

(1) Deltoids : medium sized, more or less triangular forms centred on *C. listeri.*
(2) Ovoids : small more or less ovate forms with subcentral umbones, centred on *C. ovalis.*
(3) Concinnoids : large elongate forms with beaks on the anterior quarter, centred on *C. concinna.*
(4) Rugoids : ovoids with rugose growth lamellae, centred on *C. toriyamai.*

To many workers this grouping might suggest taxa of subgeneric level, but the present writer is not convinced that general outline alone is a sufficient basis for proposing formal supra-specific taxa. Nevertheless, these informal morphologically descriptive terms, deltoids, ovoids, concinnoids and rugoids, are useful in discussion and, lacking formal status, they avoid trinomialism and add nothing to the 'jungle of nomenclature'.

Work on the Middle Lias of the Dorset Coast (Palmer 1962) and of Gloucestershire (Palmer 1972) led to the discovery of three undescribed forms of *Cardinia.* One of these came from the Margaritatus Zone of Gloucestershire, the other two from the Margaritatus and Spinatum Zones of Dorset. The Gloucestershire specimens, though only 45 mm in length, resemble the equivalent growth stage of the stratigraphically higher *Cardinia concinna* but differ in their shorter length-to-height ratio and smaller size. The Dorset forms bear a remarkable resemblance to *Cardinia toriyamai* described by Hayami (1958) from the Lower Liassic Higashinagano Formation in Yamaguchi Prefecture, west Japan. The earliest of the Dorset shells were found together with many small immature bivalves in Day's Shell Bed, which lies a few feet below the better-known Starfish Bed at the top of the Eype Clay in the

Stokesi Subzone of the Margaritatus Zone (Howarth 1958). Attempts to match these shells with other specimens of *Cardinia* in the collection of Mesozoic bivalves in the British Museum (Natural History) proved futile, except for one specimen of *Cardinia rugulosa* Tate 1875, from Munger Quarry, Radstock, and two others collected by J. W. Tutcher and J. Etheridge from the Spinatum Zone, in the Marlstone Layer of the Junction Bed, Dorset. The last resembled no previously described European forms of *Cardinia* and differed only slightly from the stratigraphically older Shell Bed specimens and those from Radstock.

The 23 species of *Cardinia* recognized as occurring in the British Lias are grouped in four categories according to their general appearance. Hayami (1958 : 117–118) divided the genus into six groups, prefixing each with the characteristic species of that group (e.g. 'Concinna-group', 'Crassissima-group' etc.). The number of divisions seems extravagant when apparently four will suffice, at least for the British species which are listed as follows

Deltoids

Cardinia with a more or less trigonal outline corresponding with Hayami's 'Hybrida-group'. They include the following British species :

C. listeri (J. Sowerby 1817), Lower Sinemurian . . . Pl. 1, figs 1–3
C. hybrida (J. Sowerby 1817), Hettangian–Sinemurian Pl. 1, figs 5–8 ; Pl. 3, fig. 7
C. imbricata (Stutchbury 1842), Sinemurian . . . . Pl. 1, figs 11–13
C. subabducta sp. nov., Sinemurian . . . . . Pl. 1, figs 9–10
C. raasayi sp. nov., Upper Sinemurian . . . . . Pl. 1, fig. 4
C. ingens Tawney 1866, Hettangian . . . . . Pl. 5, fig. 7
C. crassissima (J. Sowerby 1817), Upper Domerian . . . Pl. 4, figs 1–2
C. idalia d'Orbigny 1850, Upper Domerian . . . . Pl. 4, fig. 3
C. slatteri Wilson & Crick 1889, Lower Whitbian . . . Pl. 5, figs 8–10

(*Nidarica* Cox (1961 : 335), proposed for *C. slatteri*, is treated as a synonym of *Cardinia* below and *slatteri* is here grouped with the deltoids.)

Ovoids

Cardinia with ovate outline corresponding, in part, with Hayami's 'Toriyamai-group'. They include the following British species :

C. crassiuscula (J. Sowerby 1817), Lower Sinemurian . . . Pl. 2, figs 7–10
C. ovalis (Stutchbury 1842), Hettangian . . . . . Pl. 2, figs 1–3
C. huntcliffensis sp. nov., Domerian . . . . . Pl. 3, fig. 8
C. laevis (Young & Bird 1828), Domerian . . . . . Pl. 3, figs 4–6
C. subobovata sp. nov., Hettangian . . . . . Pl. 4, fig. 6
C. suttonensis Tawney 1866, Hettangian . . . . . Pl. 5, fig. 6

Concinnoids

Elongated *Cardinia* corresponding with Hayami's 'Concinna-group' but, owing to his wrong citation of type species of *Cardinia* (1958 : 117), they are not '*Cardinia* sensu stricto' of his own classification. The British species are :

C. concinna (J. Sowerby 1819) Upper Domerian–Lower Whitbian Pl. 3, figs 1–2
C. gigantea (Quenstedt 1856), Lower Sinemurian . . . Pl. 3, fig. 3
C. lanceolata (Stutchbury 1842), Lower Sinemurian . . . Pl. 2, fig. 4
C. attenuata (Stutchbury 1842), Carixian . . . . Pl. 2, figs 5–6
C. tuffleyensis sp. nov., Domerian . . . . . Pl. 4, figs 4–5

Rugoids

Cardinia with ovate outline and imbricating growth lamellae, some with upturned edges. These correspond, in part, with Hayami's 'Toriyamai-group' and include the following British species:

C. rugulosa (Tate 1875), Carixian . . . . . Pl. 5, fig. 5
C. dayi sp. nov., Lower Domerian . . . . . Pl. 5, fig. 3
C. tutcheri sp. nov., Upper Domerian . . . . . Pl. 5, figs 1–2

Table

The stratigraphical zones and stages of the British Lias proposed by Dean, Donovan & Howarth (1961) and used in this study

ZONES	STAGES	LITHOLOGY	
Levesquei Thouarsense	Yeovilian (Upper Toarcian)	Sands and marls	Upper Lias
Variabilis Bifrons Falciferum	Whitbian (Lower Toarcian)	Shales and marls passing southwards into thin limestones and nodules	
Tenuicostatum		Transition Bed	
Spinatum	Domerian (Upper Pliensbachian)	Marlstone Rock Bed	Middle Lias
Margaritatus		Sandy shales	Middle Lias of some 19th century authors
Davoei Ibex Jamesoni	Carixian (Lower Pliensbachian)	Silty shales	
Raricostatum Oxynotum Obtusum Turneri Semicostatum Bucklandi	Sinemurian	Marls and shales Frodingham Ironstone Shales and paper-shales	Lower Lias
Angulata Liasicus Planorbis	Hettangian	Shale and limestone alternations – 'Blue Lias'	

The Table shows the stratigraphical zones and stages of the British Lias used in this study. The column headed 'Lithology' is generalized and simplified but usually the lowest four zones are in limestone and shale alternations – a division usually known as the 'Blue Lias'. This is succeeded by paper-shales and shales around the Semicostatum and Turneri Zones. The rest of the Lower Lias is in shale and marl which becomes more silty around the Davoei Zone, and sandy in the Margaritatus Zone of the Middle Lias. The Marlstone Rock Bed is widespread and corresponds with a profound change in the Liassic fauna. The succeeding Transition Bed marks the highest reliable record of British *Cardinia*.

II. TRIVIAL NAMES USED WITH *CARDINIA*

In proposing new names for *Cardinia* species the following trivial names were discovered to have previously appeared in publication in combination with the generic name *Cardinia*. It is basically Hayami's list (1958 : 123–127) but with additions by the present author. No claim is made for its completeness but only that these names at least can be avoided by other workers. New species described herein are indicated *.

abductus
acuminata
amurensis
amygdala
andium
angustata
angustiplexa
antiqua
aptychus
aritiensis
attenuata
authelini

bensoni
breoni
brevis

chillyensis
collenoti
concinna
conjugensis
contracta
copides
cordata
crassissima
crassiuscula
cuneata
cyprina

**dayi*
densistriata
depressa
deshayesi
desoudini
dormali
dunkeri

elliptica
elongata
eveni
exigua
exilis

fischeri
follini

gibba
gibbosula
gibbosum
gigantea
gleimi
gottingensis

hennocquii
**huntcliffensis*
hybrida

idalia
imbricata
inexpectans
infera
ingelensis
ingens
insignis
itea

keuperiana
koninckii
kullensis
laevis
lamellosa
lanceolata
latiplex
latitruncata
lerichei
listeri
lucinaeformis
lycetti

mactroides
minor
misawensis
moreana
morisi

nachamensis
nilssoni
nostra

oblonga
obovata
oppeli
ovalis
ovula
ovum

philea
piriformis
plana
ponderosa
porrecta

quadrangularis
quadrata
**raasayi*
regularis
rhyckholti
rugulosa

scapha
scutula
securiformis
siberica
similis
sinemuriensis
slatteri
**subabducta*
subacuminata
subaequilateralis
subangulata
sublamellosa
**subobovata*
subovalis
subtrapezoides
sulcata
suttonensis

tas-aryensis
toriyamai
trapezium
triadica
trigona
**tuffleyensis*
**tutcheri*

unioides

wyomingensis

zeilleri

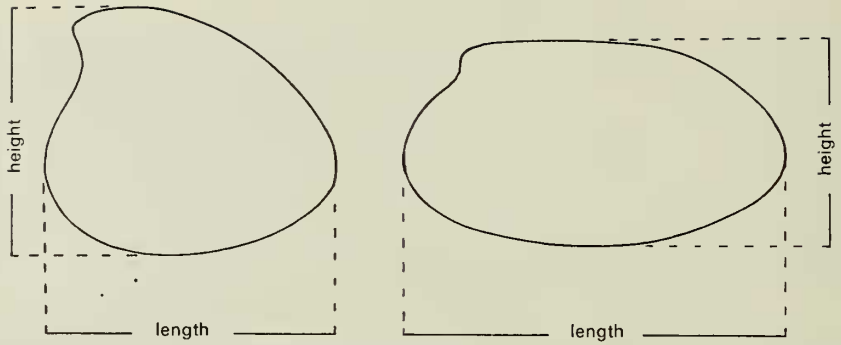

FIG. 1. Measurements of *Cardinia* : left figure a deltoid, right figure a concinnoid. Length is measured along the longitudinal axis, i.e. the greatest distance between the anterior and posterior margins. In *Cardinia* the longitudinal axis is usually parallel to a line joining the anterior and posterior laterals. Height is measured at right angles to the length.

III. HINGE NOTATION

The internal structures forming the hinge of *Cardinia* are remarkably constant in position and character. The typical pattern comprises in the right valve a more or less obsolete cardinal tooth 3b, usually no more than an elongated low swelling,

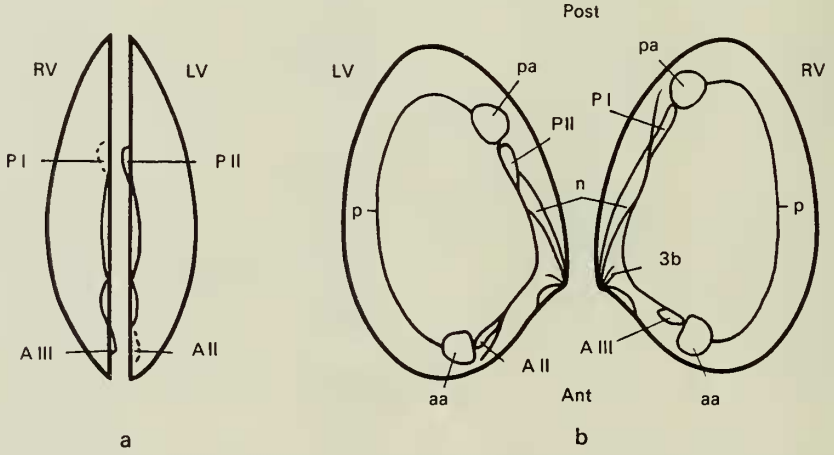

FIG. 2. (a) Articulation of the lateral teeth in the valves of *Cardinia crassiuscula* drawn, with the dorsal margin uppermost, from specimens from the Frodingham Ironstone of Scunthorpe, Lincolnshire, $\times \frac{1}{2}$. The dotted teeth lie ventral to teeth with solid lines. (b) Internal left and right valves of *C. crassiuscula* from the Frodingham Ironstone of Scunthorpe, Lincolnshire, $\times \frac{1}{2}$. Symbols for both figures are as follows : LV, left valve ; RV, right valve ; Ant, anterior ; Post, posterior ; n, ligamental nymph ; p, pallial line ; aa, anterior adductor muscle scar ; pa, posterior adductor muscle scar ; 3b, position of obsolescent cardinal tooth ; AII, anterior lateral tooth in left valve ; AIII, anterior lateral tooth in right valve ; PI, posterior lateral tooth in left valve.

well-developed lateral teeth consisting of an anterior lateral tubercular tooth, and a posterior lamellar tooth forming a socket between itself and the edge of the shell. In the left valve there is a depression to receive the obsolescent cardinal 3b but no trace of other cardinals, an anterior lateral forming a socket between itself and the edge of the shell to receive the anterior lateral in the right valve, and a posterior lateral tubercular tooth which fits into a socket formed by the posterior lateral tooth and the edge of the shell in the right valve.

Cox (1961 : 327, fig. 1) published a figure of the internal dentition of *C. hybrida* and reproduced Douvillé's (1921 : 117–118) application of the Munier-Chalmers–Bernard (1895) hinge notation to *Cardinia*. Cox remarked (p. 328) that the upper anterior lateral in the right valve, AIII of Douvillé, was not recognizable by him in the specimens he had examined, a statement which is entirely supported by the present author's experience. Douvillé depicts two anterior laterals and notates them AI and AIII ; the last, if it does not correspond to the edge of the shell, is entirely imaginary. In order to discover the relationships of the anterior and posterior laterals several complete and articulated specimens of *C. hybrida*, *C. concinna* and *C. ovalis* were sectioned so that the plane of the cut passed vertically through the laterals. These sections revealed the unsatisfactory state of Douvillé's application of the Bernard hinge notation since, in all cases, AII in the left valve was ventral to AI in the right. The numbering of lateral teeth should begin with the lowest (most ventral) tooth upwards (Cox 1969 : N53). Hence the anterior lateral in the right valve should be designated AIII (= AI of Douvillé) and Douvillé's 'AIII' does not exist, or it corresponds with the edge of the shell.

In the right valve the posterior lateral is ventral to the tubercular tooth PII in the left valve and it is correctly designated PI by Douvillé, but no tooth, unless it be

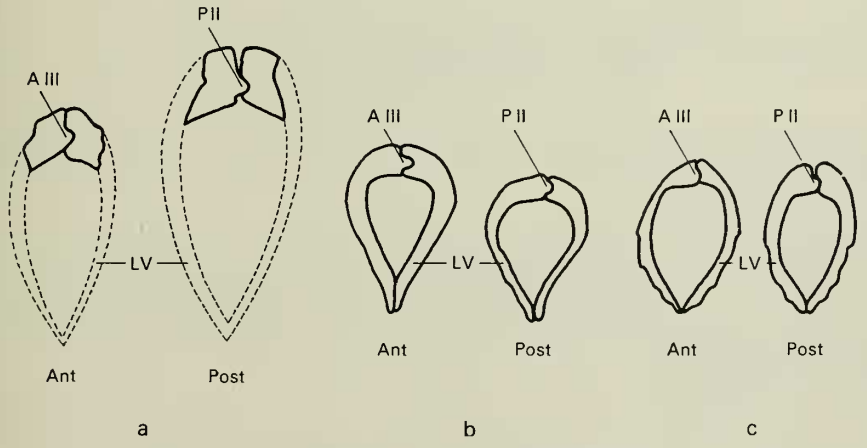

FIG. 3. Sections through lateral teeth of :
(a) *Cardinia concinna* from the Margaritatus Zone of Stonehouse, Gloucestershire.
(b) *C. attenuata*, locality and horizon unrecorded ; B.M.(N.H.) duplicate collection.
(c) *C. ovalis*, locality and horizon unrecorded. B.M.(N.H.) duplicate collection.
Notation as for Fig. 2. × ½.

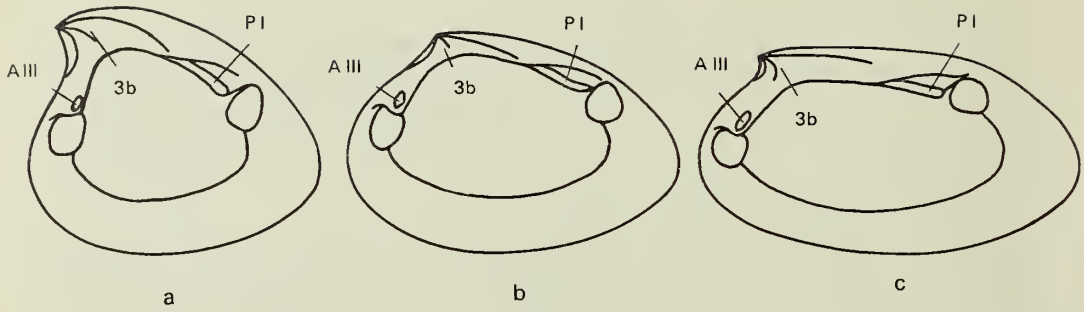

FIG. 4. Comparative hinges of right valves of :
(a) *Cardinia listeri*, Sinemurian of Evesham, Worcestershire.
(b) *C. ovalis*, Hettangian of Chadbury, Worcestershire.
(c) *C. concinna*, Whitbian, Transition Bed, Astrop, Northamptonshire.
The constancy of the dentition is well demonstrated, in spite of difference of stratigraphical age in 4b and 4c, and difference of shape in 4a and 4c. Notation as for Fig. 2. × ½.

the edge of the shell, is visible above PI, hence the 'PIII' of Douvillé does not exist. Unfortunately Douvillé failed to reveal the fact that in *Cardinia* the lateral teeth and sockets alternate, the anterior right tooth fitting into the anterior left socket, and the posterior left tooth into a posterior right socket. This arrangement forms a very powerful shear-resistant articulation for the two valves, and its permanence throughout the stratigraphical range of the genus argues for powerful selective forces maintaining this unique form of hinge.

IV. BRITISH LIASSIC SPECIES OF *CARDINIA*

Family **CARDINIIDAE** Zittel 1881

Genus ***CARDINIA*** Agassiz 1841

(= *Thalassides* Berger 1833, suppressed I.C.Z.N. ; *Ginorga* Gray 1840, *nom. nud.* ; *Sinemuria* de Christol 1841, suppressed I.C.Z.N. ; *Pachyodon* Stutchbury 1842 ; *Dihora* anon. 1842 ; *Storthodon* Zittel 1881 ; *Nidarica* Cox 1961.)

TYPE SPECIES. *Unio listeri* J. Sowerby 1817, designated I.C.Z.N. Opinion 292. The generic name was validated in the same opinion (see Cox 1951).

DIAGNOSIS. Integripalliate heterodont bivalve molluscs with unique hinge consisting of anterior laterals AII and AIII, posterior laterals PI and PII, and an obsolescent cardinal 3b.

REMARKS. The genus *Nidarica*, proposed by Cox (1961), type species *C. slatteri* Wilson & Crick 1889, is here considered to be a synonym of *Cardinia* Agassiz 1841. The external shell features distinguishing it from other cardiniids, concave lateral surfaces and very incurved beaks, are only an extension of a trend already visible in the earlier deltoid *C. idalia* d'Orbigny. The hinge differs in no significant way from that of other species of *Cardinia*.

Cardinia listeri (J. Sowerby 1817)

Plate 1, figs 1–3

1817 *Unio listeri* J. Sowerby : 123, pl. 154, figs 1, 3, 4.
1842 *Pachyodon listeri* (Sowerby) Stutchbury : 482, pl. 9, figs 1, 2.
1849 *Cardinia listeri* (Sowerby) Brown : 213, pl. 74, fig. 20 (only).
1962 *Cardinia listeri* (Sowerby) Castell : 64, pl. 10, fig. 2.

Material. In the British Museum (Natural History) are two syntypes : one corresponding to Sowerby's fig. 1 'sent me from Durham, as found in that neighbourhood some years since in Clayey Limestone' ; and another, fig. 4, collected by a Mr Strangeways from Scarborough. Since Lias is known at neither of these localities the following explanations are offered. Specimens resembling the syntypes were collected by J. F. Blake from the Bucklandi Zone of Redcar, Yorkshire. Redcar is but 20 miles from Durham and a collector living in that city might have visited Redcar and sent the specimen collected to Sowerby 'from Durham'. Around Scarborough Middle and Upper Jurassic is overlain by Boulder Clay which seems to have been a rich source for Jurassic fossils – and possibly of Sowerby's other syntype. The specimen corresponding to Sowerby's pl. 154, fig. 1 (the 'Durham' specimen) is here selected lectotype leaving the other (the 'Scarborough' specimen) as paralectotype. Dimensions of lectotype, B.M.(N.H.) Pal. Dept. LL 31297 : height 44 mm ; length 50 mm ; inflation 23 mm ; h/l = 87·5% (Pl. 1, fig. 1). Dimensions of Paralectotype, B.M.(N.H.) 43221 : height 40 mm ; length 50 mm ; inflation 21 mm ; h/l = 80·0% (Pl. 1, fig. 2).

Description. Sowerby's description is 'cordate, transversely imbricated, beak recurved, acute ; posterior side small ; middle flattish ; shell thick'. The types are subtrigonal in outline, slightly prosogyrous, beaks on the anterior quarter of the length ; shell moderately inflated with the anterior margin slightly concave. The shell is covered with about 18 fairly regularly spaced, concentric growth imbrications between shell heights 8 mm and 44 mm.

The hinge consists of a massive and strongly arched hinge plate containing, in the right valve, an obsolescent cardinal tooth 3b, a tubercular anterior lateral AIII, and an elongated posterior lateral PI making a socket for the reception of the posterior lateral tooth of the left valve. The left valve contains a barely perceptible fold for the reception of 3b of the right valve ; a tubercular anterior lateral AII forms a socket, with the edge of the shell, for the reception of AIII in the right valve ; an elongated and tubercular posterior lateral PII fits into a socket formed in the right valve by PI and the edge of the shell. A deeply sunk ligamental nymph lies posterior to the beaks and above the summit of the arch formed by the hinge plate.

Both the anterior and posterior adductor muscle scars are fairly well impressed, causing the ends of the hinge plate to be abruptly truncated and terminating in a vertical wall from the top of the hinge plate down to the muscle scar. An entire pallial line is usually well displayed and makes a regular curve from the anterior adductor towards the posterior adductor, which it passes ventrally, curving sharply

back to meet it from a postero-ventral direction. A rather deeply impressed lunule lies beneath the incurled beaks.

Comparisons. This differs from *C. hybrida* in its more elevated shell, and from *C. raasayi* sp. nov. in its flatter ventral margin and smoother shell.

Horizon and Localities: Range probably Bucklandi–Obtusum Zones in the Sinemurian Stage. It has been reported from: 1·2 km (¾ mile) west of Watchet, Somerset; Cheltenham and Stonehouse (not the quarry), Gloucestershire; Bengeworth and Evesham, Worcestershire; Warkworth and Welford, Northamptonshire; in the Frodingham Ironstone at Scunthorpe, Lincolnshire; Redcar, Yorkshire.

Cardinia hybrida (J. Sowerby 1817)

Plate 1, figs 5–8: Plate 3, fig. 7

1817 *Unio hybrida* J. Sowerby: 124, pl. 154, fig. 2.
1833 *Unio depressa* Zieten: 81, pl. 61, fig. 1a–d.
1842 *Pachyodon cuneatus* Stutchbury: 484, pl. 10, figs 11, 12.
1842 *Pachyodon hybrida* (Sowerby) Stutchbury: 482, pl. 9, figs 3, 4.
1849 *Cardinia listeri* (Sowerby) Brown: 214, pl. 74, fig. 19 (only).
1962 *Cardinia hybrida* (Sowerby) Castell: 64, pl. 10, fig. 2.

Material. Sowerby's holotype, fig. 2, B.M.(N.H.) 43222, is recorded by him from Nottinghamshire, whence it came either from the Lower Lias or from Boulder Clay. If the latter, then comparison with specimen B.M.(N.H.) L 28722, from Robin Hood's Bay, a block with three specimens exposed, indicates that the origin may have been Yorkshire. Dimensions of holotype, B.M.(N.H.) 43222: height 28 mm; length 42 mm; inflation 15 mm (crushed); h/l = 66·5% (Pl. 1, fig. 5).

Description. Sowerby's terse description is: 'oblong, ovate, anterior side subacuminate; surface imbricated; breaks recurved, acute; shell thick', and needs little amplification except to add that the imbricating lamellae are slightly undercut, the posterior often pointed, and the lunule rather deeply excavated and, in some cases, bounded by a ridge. The hinge teeth are exactly as in *C. listeri* only smaller, and the hinge plate, owing to the more depressed outline of the shell, forms a flatter arch.

Comparisons. Zieten's *Unio depressa*, from the Upper Sinemurian and Lower Pliensbachian of Deyerlock and Vaihingen near Stuttgart, Württemberg, is a slightly more depressed form of *C. hybrida*. In Britain it occurs most abundantly in the Lower Lias of Gloucestershire and Worcestershire where it shows complete gradation into the true *hybrida*-form. *C. hybrida* differs from *C. listeri* in being consistently more depressed with a h/l ratio of 66·5% compared with 87·5% in *C. listeri*. *C. depressa* (Pl. 1, figs 7–8) is here treated as a variety of *hybrida*.

Stutchbury's *Pachyodon cuneatus*, here figured on Pl. 3, fig. 7, is indistinguishable from *C. hybrida*. The type is from the 'Lias of Fretherne, Gloucestershire' and the species is recorded from bed 12 by Richardson (1908) which is but 150 cm (5 ft) below a limestone yielding *Arnioceras bodleyi*. This, together with the detailed work of Henderson (1934), confirms that it came from the Semicostatum Zone.

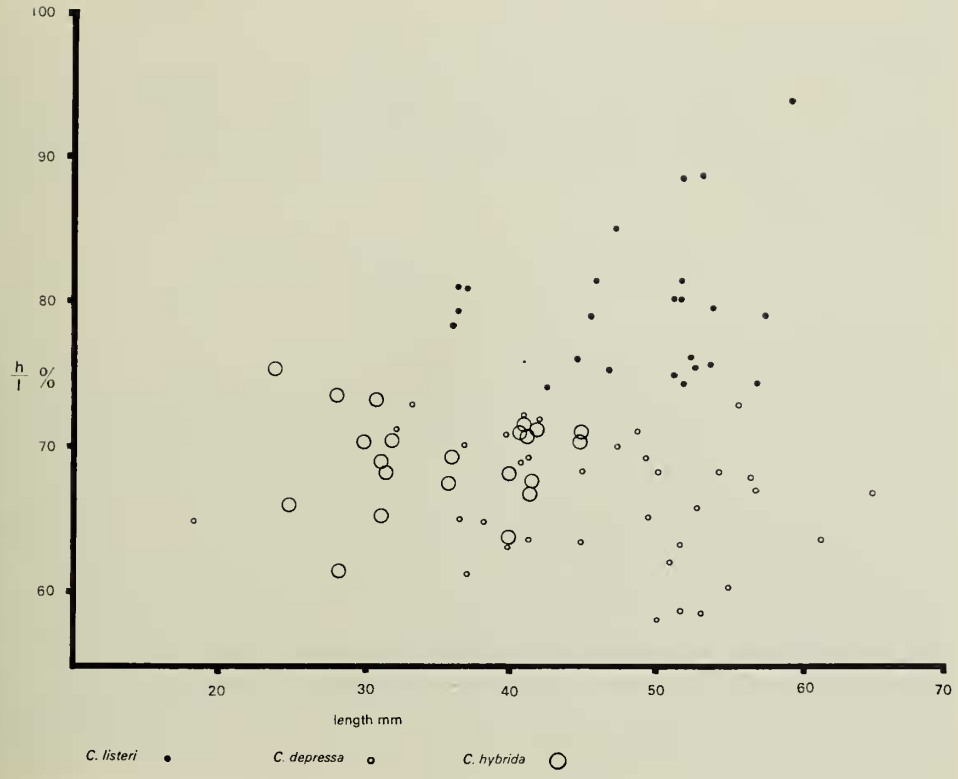

FIG. 5. The relationships of the three forms *Cardinia listeri*, *C. depressa* and *C. hybrida* expressed by their height : length ratios. *C. listeri* has a scatter distribution wholly above that of the *depressa–hybrida* group. Generally, *C. depressa* attains a larger size than *C. hybrida* and it is then that it assumes its characteristic shape. *h/l* % = height as a percentage of the length in Figs 5–8.

The stratigraphical horizon is confirmed by the B.M.(N.H.) specimen L 28721, from Redmile, Leicestershire, which is preserved in a block of Frodingham Ironstone, assigned by Hallam to the Semicostatum–Obtusum Zones, and which closely resembles Stutchbury's type figure. *C. listeri* (J. Sowerby) is a tall shell and *C. depressa* (Zieten) is, as the trivial name implies, depressed. Inevitably some *C. listeri* are less tall and some *C. depressa* are less depressed. *C. hybrida* seems to be just a smaller version of *C. depressa* and the two form a graded series. Hence a collection of these deltoids gives the impression of being 'all the same species', that is they are morphologically diverse but constitute a graded series. In order to test whether or not this was the case a height–length ratio graph was constructed and the dimensions of all available specimens, identified by conventional method of judgement, were entered upon it. Fig. 5 shows from left to right increasing length and from bottom to top increasing 'tallness' (height/length percentage) of shells.

It is clear that the *listeri* distribution lies wholly above the *hybrida–depressa* gradation.

Horizons and Localities. Range, probably Upper Angulata Zone in Hettangian Stage (Worcestershire) to Raricostatum Zone in Sinemurian stage (Scotland). Recorded from Gloucestershire ; Wilmcote and Binton, Warwickshire ; Fladbury, Bengeworth and Honeybourne, Worcestershire ; Redmile, Leicestershire ; Redcar, Yorkshire.

Cardinia imbricata (Stutchbury 1842)

Plate 1, figs 11–13

1842 *Pachydon imbricatus* Stutchbury : 483, pl. 9, figs 5, 6.

Material. Holotype in City Museum, Bristol, reg. no. C 2151, and two right valves in B.M.(N.H.). Dimensions of figured specimen, B.M.(N.H.) L 78419 : height 26 mm ; length 36 mm ; inflation 18 mm ; h/l = 73% (Pl. 1, fig. 11).

Description. 'Shell subtriangular ; lines of growth thin-edged, imbricated and numerous ; lunule cordate ; height 1·1, length 1·5, thickness 0·7. Lias, Banks of Severn, Gloucestershire, and Bishport, Somersetshire' (Stutchbury 1842 : 483). This is ovately trigonal in outline with a convex dorsal and ventral margin and a straight anterior descending rather steeply from the prosogyrous beaks. The shell surface is covered with numerous closely spaced, thin, imbricating lamellae. Lunule rather deeply excavated and bounded by a sharp ridge. Hinge as in *C. listeri*.

Comparisons. The species differs from *C. listeri* in the more closely spaced growth imbrications, the flatter anterior margin and the more convex dorsal outline giving it a 'hump-backed' appearance.

Horizon and Localities : ? Bucklandi–Semicostatum Zones in Sinemurian Stage ; Gloucestershire–Somersetshire. Recorded from Bishport, Somerset ; Fretherne and Hatherley railway cutting 2·4 km (1½ miles) south-west of Cheltenham, Gloucestershire.

Cardinia subabducta sp. nov.

Pl. 1, figs 9, 10

1842 *Pachyodon abductus* (Phillips) Stutchbury : 484, pl. 10, figs 9, 10 (non *Unio abductus* Phillips 1829).

Specific name. Alluding to *Pachyodon abductus* (Phillips 1829).

Material. Holotype in City Museum, Bristol, reg. no. C 2158, and one specimen, L 382, in B.M.(N.H.). Dimensions of L 382 : height 28 mm ; length 38 mm ; inflation 16 mm ; h/l = 74% (Pl. 1, fig. 9).

Diagnosis. Deltoid *Cardinia* resembling *C. listeri* but differing in its flatter dorso-ventral outline, sharper and less incurled beaks, and more acutely rounded anterior.

Description. Distinctly trigonal in outline with acutely pointed beaks, hardly incurled, and placed on the anterior quarter of the length. The postero-dorsal

margin is nearly flat and meets the slightly convex venter on a sharply rounded posterior curve. The anterior is more broadly rounded than the posterior, becoming concave at the rather deeply impressed lunule. Hinge exactly as in *C. listeri*. Shell surface covered with close and regularly spaced growth halts.

Comparisons. Differs from *C. listeri* in its flatter postero-dorsal margin, sharper and less incurled beaks, and more acutely rounded anterior. From *C. hybrida* it differs in being more elevated, more trigonal in outline, and having a flatter dorsum.

Remarks. Stutchbury (1842 : 484) mistakenly believed his *Pachyodon abductus* to be the same as Phillips' *Unio abductus* – an Inferior Oolite *Gresslya*. Stutchbury consequently recorded this from the 'Inferior Oolite, Dundry Hill, Somersetshire' and from the 'Lias, near Cheltenham'. This misidentification, together with the misidentification of the Marlstone at Cropredy as 'Inferior Oolite', is responsible for the long-held belief that the genus *Cardinia* ranged up into the Inferior Oolite. Although the specific name is not preoccupied in either *Pachyodon* or *Cardinia*, article 49 of the I.C.Z.N. Code requires that a new name be applied to this otherwise well-known form.

Horizon and Localities. Stutchbury (1842 : 484) records it from the 'Lias near Cheltenham'. The B.M.(N.H.) specimen, L 382, is labelled 'Lower Lias of Gloucestershire, Tennant Colln' and is associated with an older label reading 'Lower Lias, Evesham'. Attached to the specimen is a *Gryphaea* belonging to the *G. obliquata* group and this, together with the Evesham locality, suggests that it came from a horizon high in the Angulata Zone or low in the Bucklandi Zone, Hettangian to Sinemurian stages. Gloucestershire and Worcestershire seem to be the known limits of its distribution.

Cardinia raasayi sp. nov.

Plate 1, fig. 4

1843 ? *Cardinia laevis* Agassiz : 226, pl. 12″, figs 13–15 (non *Cardita laevis* Young & Bird 1826).

Specific name. From the island of Raasay.

Material. Holotype, B.M.(N.H.) L 76713, sole specimen from the island of Raasay, Inverness-shire, Scotland. Dimensions : height 50 mm ; length, 63 mm ; inflation, 27 mm ; h/l = 79·5%.

Diagnosis. Deltoid *Cardinia* resembling *C. listeri* but differing in its more convex ventral margin, less incurled and more prominent umbones, and a shell surface lacking the prominent growth halts of typical *C. listeri*.

Description. Ovately trigonal outline with broadly convex ventral margin ; umbones prominent and beaks incurled and placed on the anterior quarter of the length ; lunule excavated beneath the incurled beaks ; shell surface covered with closely spaced plications and a few widely spaced, faint growth halts. Internal characters not seen.

Comparisons. This species can only be compared with *C. listeri*, which it closely resembles but from which it differs in the characters cited above. Its distinct

shape and higher stratigraphical horizon indicate that it should be regarded as a separate species. Nevertheless, the holotype is the only example known to the author and it is impossible to say if the range of variation of the species and that of *C. listeri* might not overlap.

Horizon and Locality. Raricostatum Zone in the Sinemurian Pabba Shales ; banks of Allt Fearns, Raasay, Inverness-shire.

Cardinia ingens Tawney 1866

Plate 5, fig. 7

1866 *Cardinia ingens* Tawney : 86, pl. 4, fig. 2.

Material. Holotype in Institute of Geological Sciences, London, 91989. No other material seen ; specimen not well enough preserved for measurement.

Description. The type is an internal mould of a relatively large deltoid, and Tawney claimed (p. 86) 'that the shell was crumbly but showed strong concentric folds of growth. It approaches nearest to *C. crassissima* of Agassiz' (non Sowerby). This species, together with his *C. suttonensis*, is from the Sutton Series of south Wales and the horizon is probably low in the Hettangian.

With only a poorly preserved internal mould to hand it is impossible to describe this form or to identify, or compare, it with any described species. The mould has two prominently raised muscle platforms indicating that the adductors were deeply set into the shell. The pallial line is clearly seen, but the hinge area is covered with a secondary growth of crystals. Until better preserved material is available this species must remain in abeyance as a *nomen dubium*.

Horizon and Locality. Hettangian, Sutton Stone, Planorbis–Liasicus Zone ; Llangan, near Brocastle, Glamorgan, south Wales.

Cardinia crassissima (J. Sowerby 1817)

Plate 4, figs 1, 2

1817 *Unio crassissimus* J. Sowerby : 121, pl. 153.
1849 *Cardinia crassissima* (Sowerby) Brown : 214, pl. 74, fig. 8.

Material. Holotype, one left valve, B.M.(N.H.) 43219, and other examples in B.M.(N.H.). Dimensions of holotype : height 62 mm ; length 88 mm ; inflation 38 mm ; h/l = 70·5% (Pl. 4, fig. 1).

Description. Sowerby's description is 'Ovate, transversely undulated or imbricated ; beak recurved, acute posterior [i.e. anterior] side obscurely subcuneiform ; shell very thick'. The dorsal outline is evenly convex and, like *C. imbricata*, has a 'hump-backed' appearance. The ventral margin is relatively flatter and passes, in an even curve, into the steeply sloping and short anterior. The strongly prosogyrous beaks lie on the anterior ninth of the length and are slightly incurled over a slightly excavated lunule.

Comparisons. From *C. idalia* and *C. listeri* it differs in its more depressed and ovate outline and the absence of a strong posterior carina. From *C. idalia* it differs in its lesser inflation and relatively flatter valves.

Discussion. Examination of Sowerby's holotype leaves no doubt that Stutchbury (1842) confused two different forms when he identified his pl. 9, fig. 7 with Sowerby's *Unio crassissimus*. Stutchbury's specimen is the *C. idalia* of d'Orbigny, a form which is completely distinct from, and cannot be united with, *C. crassissima*. *C. idalia* is trigonal in outline and like a large *C. listeri*, but with a prominent angle in the postero-dorsal region ; it occurs in the Marlstone of Gretton, Gloucestershire (see p. 18). *C. crassissima* is depressed, ovate and with prosogyrous beaks ; specimens in the B.M. are labelled 'Marlstone, Tail's Hill, Glos.' (Tail's Hill is near Dursley). Another specimen, B.M.(N.H.) 20166e *ex* Baker Collection, is labelled 'Middle Lias, ? Bugbrook, Northants'. If this locality is correct then the matrix, which resembles that of the Transition Bed, suggests that the range should be extended from the Spinatum up to the Tenuicostatum Zone.

The stratigraphical position of Sowerby's holotype cannot be determined from his text, which only reveals that he received it from a Dr Sutton of Norwich who gave him 'many specimens of Fossil shells as British, *without localities* [my italics–C. P. P.] among which are several of this species all formed of Carbonate of Lime'. It was Parkinson who told Sowerby (1817 : 121) that these fossils 'are usual in Gloucestershire and Wiltshire, near Bath, sometimes in the Lias Clay', but since he was not specifically referring to Sowerby's specimen the origin must remain unknown. The only specimen known of similar preservation came from Tail's Hill, near Dursley, Gloucestershire.

Placing *C. crassissima* among the deltoids requires some explanation since it clearly presents a markedly ovate outline. The umbones of ovoids are usually placed between the median line and the anterior third, as in *C. ovalis* and *C. crassiuscula*. In contrast the deltoids usually have terminal or subterminal beaks and are strongly prosogyrous. *C. crassissima* has subterminal beaks and it is therefore included in the deltoids.

Horizon and Localities. Marlstone, Spinatum Zone, Domerian Substage. Adults are recorded from Tail's Hill near Dursley, Gloucestershire ; Bugbrook, Northamptonshire ; juveniles from the 'Middle Lias' (Quarry) at Stonehouse, Gloucestershire ; Chipping Norton, Oxfordshire ; Litchborough, Northamptonshire.

Cardinia idalia d'Orbigny 1850

Plate 4, fig. 3

1842 *Unio crassissimus* Sowerby ; Stutchbury : 483, pl. 9, fig. 7 (non Sowerby).
1850 *Cardinia idalia* d'Orbigny : 235 (Prodrome no. 169).
1907 *Cardinia idalia* d'Orbigny ; Thevinin : 44, pl. 12, figs 10–12.

Material. Several examples in the B.M.(N.H.), including the specimen here figured. Dimensions of figured specimen, LL 31270 : height 67 mm ; length 81 mm ; inflation 46 mm ; h/l = 83·0%.

Description. D'Orbigny's species is from the 'Liassien' (Pliensbachian) of France. The British specimens occur in the Marlstone of Gretton, Gloucestershire, and are virtually identical with Thevinin's (1907) figures although larger. The species is trigonal in outline but with a posterior carina demarcating a siphonal area. The dorsum is straight with a sharp change of direction where the posterior carina meets the posteroventral edge. The venter merges with the anterior in a continuous concave curve which changes to a convex curve beneath the incurled and prosogyrous umbones. The flanks have a tendency to flatness suggesting the concave condition seen in *C. slatteri* (*Nidarica* Cox) from a higher horizon.

Comparisons. *C. idalia* differs from *C. crassissima* in its more trigonal outline and the bluntly angled posterior surface ; the last character distinguishes it, together with its greater size, from the earlier *C. listeri* which it otherwise resembles.

Horizon and Locality : Marlstone, Spinatum Zone, Domerian Substage of Gretton, Gloucestershire.

Cardinia slatteri Wilson & Crick 1889

Plate 5, figs 8–10

1889 *Cardinia slatteri* Wilson & Crick : 337, pl. 10, figs 1, 2.
1961 *Nidarica slatteri* (Wilson & Crick) Cox : 335, pl. 14, figs 11–13.

Material. The lectotype, O.U.M. J 14707, selected by Cox (1961), is in the Oxford University Museum together with several other examples. Dimensions of lectotype : height 25 mm ; length 28 mm ; inflation ca. 10 mm ; h/l = 89% (Pl. 5, fig. 8).

Description. 'Opis-like, with strongly prosogyrous, terminal umbones, from which [two] prominent, angular carinae, both strongly curved with a posteriorly facing convexity, pass to the extremities of the concave ventral margin. Lunule deep, angular ; nymphs not quite so deeply sunk as in [other] *Cardinia*. No distinct cardinal teeth, but in the left valve the lunular marginal region projects and is much thickened, this projection being received in a corresponding recess in the right valve' (Cox 1961 : 335). The lateral area between the two carinae is strongly concave and the surface ornament consists of well-separated growth halts.

Comparisons. Resembling *C. idalia* but smaller, beaks more prosogyrous, and unique in having a concave lateral depression between the carinae. But some specimens of *C. idalia* from the Marlstone show a tendency towards lateral flattening, which may be antecedent to the concave condition in the later *C. slatteri*.

Discussion. Cox proposed the name *Nidarica* as a monospecific genus closely related to *Cardinia*. It is the opinion of the present writer that the hinge differs in no significant way from that of *Cardinia*, and that the presence of lateral concavities in the valves does not signify a generic distinction.

Horizon and Localities. Cox recorded the species from the Transition Bed and also from the Marlstone, but it seems to me that records from the Marlstone simply reflect a lack of differentiation in the collecting of earlier workers. Matrices

examined by the present writer are all closely similar to typical Transition Bed lithology.

Transition Bed, Tenuicostatum Zone in Whitbian Substage. Aston-le-Walls and Appletree, Northamptonshire ; Tilton, Leicestershire.

Cardinia crassiuscula (J. Sowerby 1817)

Plate 2, figs 7–10

1817 *Unio crassiusculus* J. Sowerby : 191, pl. 185.
1829 *Pullastra* sp. Phillips : 161, 192.
1835 *Pullastra prototypa* Phillips : 133, pl. 13, fig. 16.
1835 *Pullastra antiqua* Phillips : 184, pl. 13, fig. 16.
1842 *Pachyodon crassiusculus* (Sowerby) Stutchbury : 483, pl. 9, fig. 8.
1849 *Cardinia crassiuscula* (Sowerby) Brown : 214, pl. 74, fig. 18.
1875 *Cardinia crassiuscula* Stutchbury ; Phillips : 254, pl. 13, fig. 16.
1875 *Cardinia antiqua* (Phillips) Phillips : 331, pl. 13, fig. 16.
1876 *Cardinia antiqua* (Phillips) Tate & Blake : 390.

Material. B.M.(N.H.) LL 31266 here designated **neotype**, collected by the author from the Frodingham Ironstone, bed 4 of Hallam (1963), about Turneri Zone ; also left and right valves, B.M.(N.H.) LL 31267–8 here figured together with the neotype. These and many others collected from the same bed at Crosby Warren, near Scunthorpe, Lincolnshire. Dimensions of neotype : height 54 mm ; length 81 mm ; inflation 32 mm ; $h/l = 67\%$ (Pl. 2, fig. 7).

Description. Sowerby's original description : 'Spec. Char. Oblong-elliptical, depressed ; valves thick ; surface marked by lines of growth ; hinge strong. The surface of this shell is regularly curved, without any hollow or rising ; the beaks are sharp, a little recurved ; the lines of growth are not very prominent, except two or three of them near the edge ; the hinge is light and elegant in comparison with that of *U. crassissimus* although thick'.

This shell is the most regularly ovoid of the British species of *Cardinia*. The beaks, slightly incurled, occupy the anterior quarter of the length, and the surface is covered with widely spaced, but irregularly placed, growth halts. As Sowerby observed, the hinge is relatively slender in construction and not so massively built or strongly arched as in *C. crassissima* and *C. idalia*. It is composed of the usual obsolescent 3b, AIII and PI in the right valve, and AII and PII in the left. The hinge plate of this species, and of all the ovoids, forms a flatter arch than in *C. listeri* and the rest of the deltoids, the teeth tending to be generally smaller. The ligamental nymph is deeply sunk and situated posterior to the beaks and slightly overlaps the posterior lateral tooth.

The lunule is bounded by a rather sharp ridge and is somewhat deeply excavated in some cases, while in others it is only moderately excavated, and the anterior slopes at about 40–45 degrees in a slightly concave line to the antero-ventral edge.

Comparisons. Resembles *C. ovalis* in outline but the beaks are more incurled, the outline more regularly ovate, the valves more evenly inflated, and the adult shell larger than that species. It is unfortunate that the similar names *crassiuscula* and *crassissima* should have caused such confusion in the minds of workers. The

two names have been applied with a careless abandon and without due regard for the shape of the shell and its stratigraphical horizon when naming specimens. *C. crassiuscula* is an ovoid resembling a large *C. ovalis* and occurring abundantly in the Frodingham Ironstone of Scunthorpe, Lincolnshire ; it occurs most abundantly in the Lower Sinemurian Stage but may range outside it. *C. crassissima* is a 'hump-backed' form, resembling a large *C. hybrida*, and more closely related to the deltoids than to the ovoids ; its prosogyrous beaks are situated on the anterior sixth of the length. It occurs sparingly in the Marlstone, Spinatum Zone, Domerian Substage of Gretton, Gloucestershire. Compare Pl. 2, fig. 7 with Pl. 4, fig. 1a.

Discussion. Attempts, both by the present writer and the late Dr L. R. Cox, to trace the missing type of *C. crassiuscula* have not been successful. It was collected by the Rev. G. R. Leathes 'from the Crag at Bawdsey' (Bawdsey, 9 miles SSE of Woodbridge, Suffolk). Stutchbury (1842 : 483) doubted the locality and hinted that it may have come from the Marlstone since the Crag and Marlstone fossils are often of a similar colour. However, S. V. Wood (1859 : 32–45) listed many Jurassic fossils derived into the Red Crag ; and in the B.M.(N.H.) collections there is a badly eroded left valve of *C. crassiuscula*, 43219, labelled 'Red Crag, Bawdsey'. A comparison of this with numerous specimens, collected by the present writer, from the Frodingham Ironstone of Scunthorpe, Lincolnshire, leaves no doubt as to the identity of Sowerby's original specimens with the Scunthorpe forms and the probable truth of the Bawdsey locality cited by Sowerby. The specimen from Bawdsey in the B.M.(N.H.) is a left valve, almost replaced by limonite, very crumbly, and obviously the result of weathering of the original blue-green chamositic preservation of the Frodingham Ironstone – from which it was almost certainly derived.

Examination of the holotype of Phillips' *Pullastra prototypa* (1835 : 133, = *antiqua* on p. 184) reveals that it is the young stage of *C. crassiuscula*. Tate (1876 : 390) was therefore wrong to identify Phillips' type with the small subtrigonal deltoids from the 'Sandy Series' (Lower to Middle Lias) of the Yorkshire coast. Phillips' type, TSP 232A in the York Museum, is labelled '*Cardinia antiqua* (Phil.) Robin Hood's Bay' (Pl. 2, fig. 10). The preservation and colour indicate a Lower Liassic rather than a Middle Liassic origin, and the locality may be correct. However, it may just as probably have come from the Lower Lias at Redcar, Yorkshire, or from the Drift.

Horizon and Localities. Semicostatum–Obtusum Zones, Sinemurian Stage. It has been reported from : Brook Down, Hatherley, Gloucestershire ; Vale of Belvoir, Leicestershire ; Crosby Warren, Yarborough and Roxby in the Scunthorpe district of Lincolnshire ; Millington, Yorkshire. It is most abundant in the Frodingham Ironstone of Lincolnshire.

Cardinia ovalis (Stutchbury 1842)

Plate 2, figs 1–3

1842 *Pachyodon ovalis* Stutchbury : 485, pl. 10, figs 17–19.
1843 *Cardinia cyprina* Agassiz : 225, pl. 12″, figs 4–6.
1843 *Cardinia unioides* Agassiz : 225, pl. 12″, figs 7–9.

MATERIAL. Stutchbury's holotype preserved in the City Museum, Bristol, C 2149, and many examples in the B.M.(N.H.) and collected by the author. Dimensions of holotype : height 32 mm ; length 46 mm ; inflation 20 mm ; h/l = 50% (Pl. 2, fig. 1).

DESCRIPTION. Stutchbury's original description (1842 : 485) is : 'Shell elliptical ; anterior margin rounded, posterior margin but little attenuated ; the lunule or depression of the anterior dorsal part small and narrow ; height 1·1, length 1·7, thickness 0·6'. These small shells are regularly ovate in outline with the beaks on the anterior third of the length. The surface is covered with irregularly spaced growth halts. The posterior part tends to become elongated in some, and, in some, a slight angle is developed in the postero-dorsal outline. The hinge plate is delicately constructed and the teeth small and tubercular. In the majority the anterior is projected in a regular rounded curve but a few tend to be slightly more bluntly rounded.

COMPARISONS. This closely resembles *C. crassiuscula* in its regularly ovate outline but differs in its tendency to elongate posteriorly, its more projected anterior outline, its tendency to develop a slight angle on the postero-dorsal outline, its small size and its stratigraphically earlier occurrence in the Hettangian. *C. hybrida* is of a similar size but is more trigonal in outline, the beaks being more prosogyrous and the anterior shorter and more steeply sloping.

DISCUSSION. Stutchbury claimed that this species occurs in the Lower Lias at Fretherne (Lower Sinemurian), but neither Richardson (1908) nor Henderson (1934) recorded it from that locality ; the present writer, who has also examined that section, failed to find it either. However, a fairly extensive collection exists in the B.M.(N.H.) and the localities suggest that this species is mainly concentrated in the 'Angulata Zone' of earlier authors (including the Liasicus Zone of Dean, Donovan & Howarth, 1961). I have collected it from Kilve in north Somerset and from a road section west of Evesham, Worcestershire ; at both these localities it is apparently confined to the Liasicus Zone and it is extremely abundant at Evesham. The evidence indicates that this is an essentially Hettangian species and the author's collecting shows that it is most abundant in the Liasicus Zone.

Agassiz, in describing two new species of *Cardinia* from Gloucestershire, was certainly aware of Stutchbury's 1842 paper, but nevertheless he proposed the name *C. cyprina* for Stutchbury's *C. ovalis* and the name *C. unioides* for the posteriorly elongated form. Fig. 6 shows the unionid form as a group of dots beyond the 50 mm length and below the 70% h/l ratio. The diagram indicates that '*C. unioides*' is the result of a tendency to elongate posteriorly in the largest individuals of *C. ovalis*, a trend which is paralleled by *C. attenuata* in the Lower Pliensbachian Ibex Zone, but in that species very much more strongly emphasized.

This species is perhaps the most variable of all the British species of *Cardinia*, but one which, nevertheless, presents few difficulties in identification since the essentially characteristic aspect of the form is always present, no matter how the dimensions change. A comparison of Figs 6 and 7 shows the wide range of variation (Fig. 6) of *C. ovalis* which is encountered in museum collections made up of specimens

from widely differing localities and horizons, and the narrower range in a collection from one locality and a narrower stratigraphical range (Fig. 7). Some of these have the posterior margin elongated and approach, but do not reach, the attenuated form of the Lower Pliensbachian *C. attenuata* from the Ibex Zone ; some are more ovate in outline and many of these have the central part inflated with the ventral margin 'pinched-in' ; some have the postero-dorsal margin regularly curved while others have a slight angle about midway to the posterior edge. Nevertheless, in all these variations the essential appearance remains and the diagrams emphasize the continuity of all the variants within the one morphospecies.

Horizons and Localities. Liasicus zone, Hettangian Stage to ? basal Bucklandi Zone in Sinemurian Stage. It is reported from : the Liasicus zone, bed H 67, in the Blue Lias west of Lyme Regis, Dorset ; Hilmorton, Wiltshire ; Lavernock, Glamorgan ; Watchet and Kilve, north Somerset ; Stretton, Gloucestershire ; Chadbury, Fladbury, Pershore and Evesham, Worcestershire ; Alcester, Binton

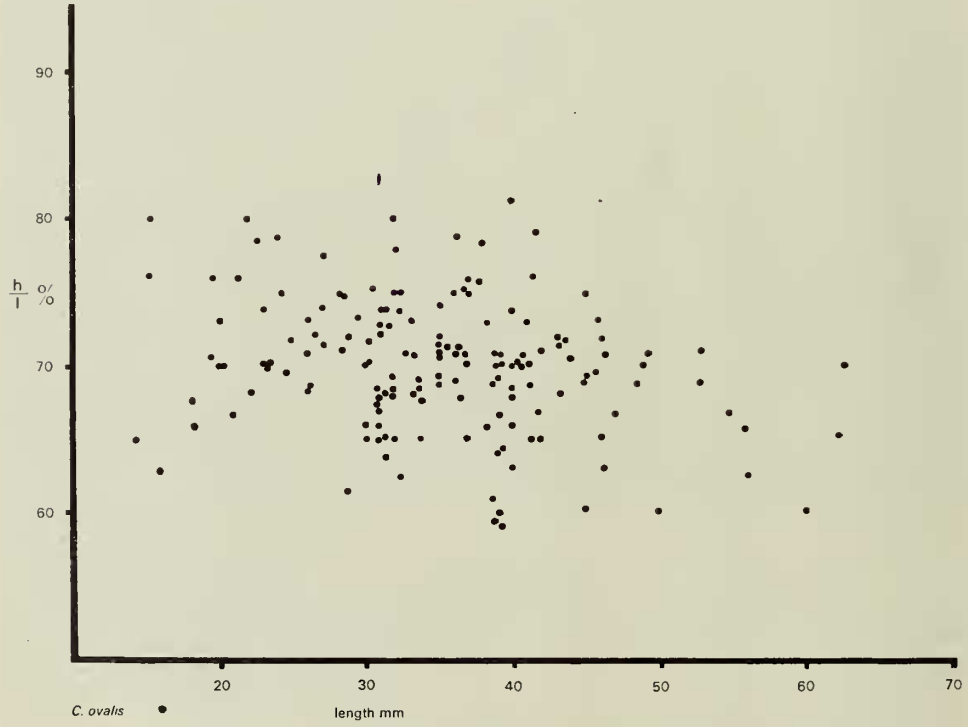

Fig. 6. All specimens of *Cardinia ovalis* in the British Museum (Natural History) were measured and plotted. They originated from various horizons in the Hettangian and their localities ranged between north Somerset and Warwickshire. The diagram demonstrates the wide morphological diversity of *C. ovalis* in large museum collections. The form *unioides* is represented by the outlying dots below and to the right. The central, upper and left-hand dots represent typical *C. ovalis*.

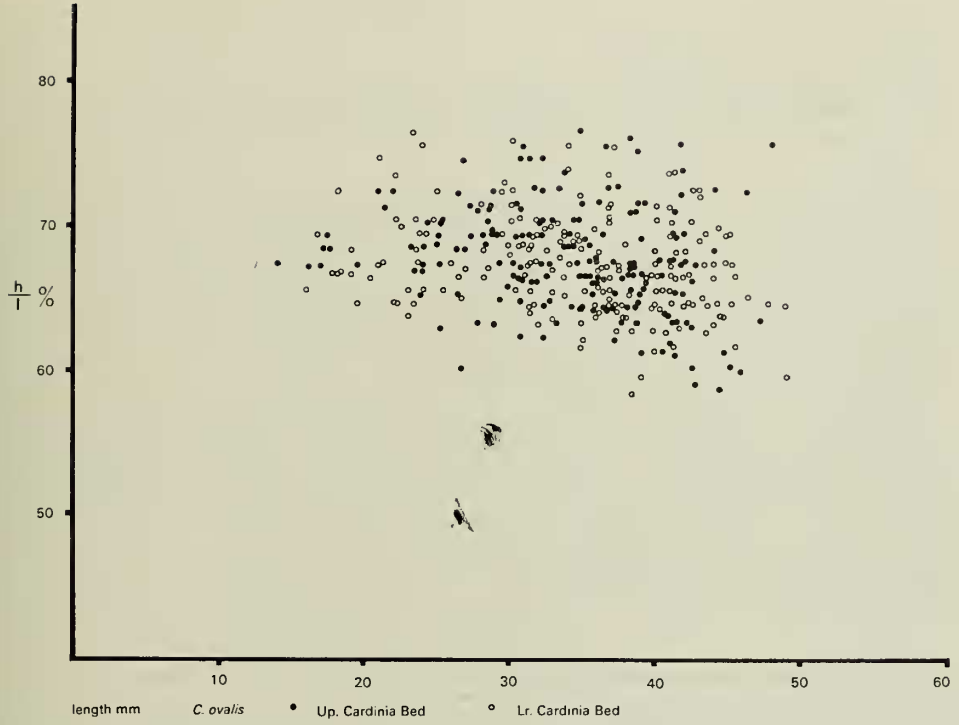

FIG. 7. In contrast with Fig. 6, a collection of *Cardinia ovalis* from one locality and horizon shows slightly reduced morphological diversity although many of the specimens suffered some degree of crushing which increased the vertical distribution on the diagram. The specimens were collected from a road cutting in the Liasicus Zone near Hampton, west of Evesham, Worcestershire. The two 'Cardinia Beds' are separated by 2–3 m of shale.

Hill and Wilmcote, Warwickshire ; Bugbrook and Kingsthorpe, Northamptonshire ; Robin Hood's Bay and Redcar, Yorkshire. Like *C. crassiuscula* in the Lower Sinemurian and *C. attenuata* in the Lower Pliensbachian, the Hettangian *C. ovalis* tends to occur very abundantly, particularly in the Liasicus Zone of Worcestershire and Warwickshire.

Cardinia huntcliffensis sp. nov.

Plate 3, fig. 8

1876 *Pullastra antiqua* Phillips ; Tate & Blake : 390.

SPECIFIC NAME. From Huntcliff on the Yorkshire Coast, see Tate & Blake (1876), figure on title page.

MATERIAL. Holotype, B.M.(N.H.) LL 23952, from the 'Margaritatus Sandstone', Margaritatus Zone, Huntcliff, Yorkshire ; also fourteen paratypes from the same

horizon and locality. Dimensions of holotype: height 16 mm, length 23 mm; inflation 9 mm; $h/l = 70\%$.

Diagnosis. Depressed ovoid *Cardinia* with subterminal umbones, differing from *C. hybrida* in its more prosogyrous beaks and from the young stage of *C. crassissima*, with which it might be confused, by its more ovate outline.

Description. Ovately cuneiform in outline, anterior short and sloping steeply to meet the slightly convex ventral edge in an even curve. The postero-dorsal outline is evenly rounded and converges towards the ventral edge which it meets at the sharply curving posterior. The surface is covered with closely spaced but irregularly placed growth halts. The lunule is small and rather shallow. The hinge is not exposed in any of the examples to hand since all are two-valved and articulated specimens. One internal mould shows two deeply set adductor muscle scars joined by an entire pallial line.

Comparisons. This small ovately cuneiform *Cardinia*, together with the trigonal *C. tuffleyensis*, is probably responsible for the records of *C. hybrida* ranging into the Middle Lias (Witchell 1882). It differs from *C. hybrida* in its more prosogyrous beaks and more closely spaced growth halts and its smaller lunule. From *C. tuffleyensis* it is at once distinguished by its less projecting and more steeply sloping anterior, and its more depressed outline. From the young of *C. crassissima* it differs in being more depressed and less trigonal in outline.

Remarks. Tate (in Tate & Blake 1876 : 390) identified these with Phillips' *Pullastra antiqua* (= *P. prototypa*) which, on examination of the holotype, is revealed to be the young of a *C. crassiuscula* from Robin Hood's Bay. Tate was extraordinarily confused about this species and about *C. antiqua* and *C. crassiuscula.* He says (p. 390), 'Both Strickland and Simpson are wrong in placing it under *C. crassiuscula* from which it is widely removed'. He was referring to Phillips' type which is identical with the equivalent growth stage of *C. crassiuscula* from the Lower Lias Frodingham Ironstone. He then continues to describe it: 'The shell is cuneiform, anterior side very short . . . ' etc., and clearly he was then describing the Middle Liassic Huntcliff cardiniids. It is possible that Tate, who never understood *C. crassiuscula* (cf. his pl. 14, fig. 4 with Sowerby's figure), thought that it was the name for the large Marlstone deltoids and from which *C. huntcliffensis* is certainly 'widely removed'.

Horizon and Localities. Domerian Substage. It is recorded from: Downcliff, Dorset, B.M.(N.H.) 67454 ex Etheridge Collection, associated with a specimen of *Pleuroceras spinatum* from the Marlstone Layer of the Junction Bed; from Chipping Norton, Oxfordshire; 0·8 km (½ mile) WNW of Upper Heyford, Northamptonshire; Huntcliff, Yorkshire.

Cardinia laevis (Young & Bird 1828)

Plate 3, figs 4–6

1828 *Cardita laevis* Young & Bird : 227, pl. 7, fig. 14.
1876 *Cardinia laevis* (Young & Bird) Tate & Blake : 391, pl. 11, fig. 12.
1961 *Cardinia laevis* (Young & Bird) Cox : 334, pl. 14, figs 3–10.

MATERIAL. The type 'has not been traced, but the specimens recorded by Tate (in Tate & Blake 1876 : 391) are in the Geological Survey Museum' (Cox 1961 : 334). The original of Cox's (1961) pl. 14, fig. 6 is here selected **neotype**. This specimen is also the original of that figured by Tate & Blake on pl. 11, fig. 12 ; IGS 7860. Dimensions : height 32 mm ; length 39 mm ; inflation 25 mm ; $h/l = 82\%$ (Pl. 3, fig. 4).

DESCRIPTION. 'Shell trigonal, compressed, subequilateral ; umbones acute, incurved, prominent, and approximate ; surface concentrically plicated and striated ; the striae numerous, lunule deep. Dimensions : height $1\frac{5}{12}$ inch ; breadth $1\frac{7}{12}$ inch ; thickness 1 inch' (Tate in Tate & Blake 1876 : 391). This uncommon and unusually smooth cardiniid is ovately trigonal in outline with a flat postero-dorsal margin, a broadly curved ventral edge passing into the round and projected anterior which is sharply concave beneath the incurled and prosogyrous beaks. The general appearance of this species is that of an arcticid heterodont but having the typical cardiniid hinge. The shell surface lacks the widely spaced and irregularly placed growth halts usually seen in *Cardinia*, and the young in consequence have been mistaken for *Astarte striatosulcata* (Cox 1961 : 335).

COMPARISONS. This species does not closely resemble any other described species of *Cardinia*. In outline it resembles *C. subabducta* but differs in its more rounded ventral and postero-dorsal outlines, and its smoother shell which develops incised growth halts only at later stages of development.

HORIZON AND LOCALITIES. Middle Lias Domerian Substage. It is reported from : Winterton, Lincolnshire ; Staithes, Hob Hill, Eston, and Upleatham, Yorkshire. Examination of matrices suggests that the majority of these occurrences are in the Spinatum Zone only.

Cardinia subobovata sp. nov.

Plate 4, fig. 6

SPECIFIC NAME. Alluding to *C. obovata* Martin 1859.

MATERIAL. Holotype, a two-valved and articulated specimen, B.M.(N.H.) L 77304, collected by J. W. Tutcher from the Angulata Zone, Maxwell Quarry, Farnborough, Somerset. No other examples have been seen. Dimensions : height 24 mm ; length 30 mm ; inflation 14 mm ; $h/l = 80\%$.

DIAGNOSIS. Ovoid *Cardinia* resembling *C. obovata* Martin but differing from that species in its greater inflation and its more elevated and more anteriorly directed umbones.

DESCRIPTION. Size small for the genus, equivalve, subequilateral ; outline subobovate with the beaks situated just anterior to the mid-line, ventral margin flattened. Anterior to the beaks the outline is concave, passing into the broad curve of the anterior margin which continues in a somewhat flattened venter to a bluntly rounded postero-ventral angle where it continues, in a regularly rounded curve, to the elevated and slightly pointed beaks. The external surface of the shell,

though abraded, shows about ten growth halts from the ventral margin up to 8 mm of the beak, beyond which the shell is too worn to see. The lunule is deeply impressed ; the ligamental nymph, just visible in the articulated holotype, is deeply inset. Internal characters not seen.

Comparisons. This species closely resembles Martin's *C. obovata* from the Hettangian of the Côte d'Or in France. But it differs in its more elevated and more anteriorly placed umbones, and in its reduced inflation. Martin's figure shows a specimen with a 20 mm inflation at a height of 25 mm.

Horizon and Locality. Hettangian, Angulata Zone at Maxwell Quarry, Farnborough, Somerset.

Cardinia suttonensis Tawney 1866

Plate 5, fig. 6

1866 *Cardinia suttonensis* Tawney : 56, pl. 4, fig. 3.

Material. Holotype in Institute of Geological Sciences, London, 7863. Specimen not well enough preserved for measurement.

Description. Tawney described it as being 'nearest in form to *C. regularis* Terquem, but the posterior is more acute than that species, larger and thicker. It is less cuneiform than *C. acuminata* Martin which it resembles'.

Discussion. A comparison of the holotype (Plate 5, fig. 6) with Tawney's figure (1866 : pl. 4, fig. 3) reveals that the figure is inaccurate and, in part, fanciful. He has restored the whole of the unexposed postero-dorsal outline and then made false comparisons with well-established forms of Terquem and Martin. Clearly the holotype, as it stands, allows neither description nor comparisons to be made and, like *C. ingens*, this form must remain, for the present, in abeyance as a *nomen dubium*.

Horizon and Locality. Sutton Series, Hettangian ; at Sutton Quarries, Glamorgan, south Wales.

Cardinia concinna (J. Sowerby 1819)

Plate 3, figs 1, 2

1819 *Unio concinnus* J. Sowerby : 43, pl. 223, figs 1, 2.
1842 *Pachyodon concinnus* (Sowerby) Stutchbury : 485, pl. 10, figs 15, 16.
1849 *Cardinia concinna* (Sowerby) Brown : 213, pl. 74, fig. 4.
1849 *Cardinia scutula* Brown : 213, pl. 88, fig. 15.

Material. Holotype, B.M.(N.H.) 43218, a single left valve, probably from the Transition Bed, Cropredy near Banbury, Oxfordshire, and many others in B.M. (N.H.). Dimensions of holotype : height 43 mm ; length 79 mm ; inflation 25 mm ; h/l = 54% (Pl. 3, fig. 1).

Description. 'Spec. Char. Transversely oblong-ovate, depressed, nearly smooth, thick ; posterior side very small ; beaks prominent, recurved. Almost three times as wide as long, regularly convex, with a gently curved back ; the thickness of the

shell is remarkable ; the lines of growth are sharp ; in other respects the surface is smooth. The front is slightly incurved near the anterior end' (Sowerby 1819 : 43). Note that where Sowerby wrote 'posterior side very small' he meant 'anterior side'.

The elongated ovate outline is broken by the slightly concave anterior margin beneath the incurled beaks, which are situated at the anterior sixth of the length. The hinge plate is similar to that of *C. crassiuscula,* but altogether larger and more solid, and the usual cardiniid dentition is present. The type is from the Transition Bed, but forms from the Marlstone below tend to be larger and more rounded ventrally although otherwise indistinguishable from the true *C. concinna* at the same growth stage. Sowerby said that it was collected by Conybeare from the Inferior Oolite of Cropredy near Banbury. Conybeare obviously mistook the Marlstone outlier in the Cherwell Valley, upon which Cropredy stands, for Inferior Oolite. He may be forgiven for this since L. Richardson (1906 : 368) admits that he nearly made the same mistake at Evercreech, Somerset.

Comparisons. Tate placed *C. lanceolata* Stutchbury in synonymy with this species, a position which cannot be upheld here since *C. lanceolata* is from the Lower Sinemurian of Yorkshire and similar to *C. gigantea,* while the present species is from the Upper Domerian and lowermost Whitbian Substage, and is morphologically distinct. It differs from *C. gigantea* in being taller, less acute anteriorly, more rounded in the postero-dorsal outline, and not having the upswept postero-ventral margin of *C. gigantea.*

Remarks. On the inside of the holotype, a left valve, a mass of matrix still adheres which differs considerably from the writer's experience of Marlstone matrix. It was compared with matrices of shells known to have been collected from the Transition Bed (Tenuicostatum Zone) of the Midlands. The buff-coloured, finely oolitic matrices were very similar, and it is suggested that Sowerby's type came from the Transition Bed – Upper Lias, Whitbian Substage. The type of *C. scutula* Brown is a typical Marlstone form which Brown wished to distinguish from the smaller Transition Bed forms, since he believed, on the evidence of Conybeare, that Sowerby's type came from the Inferior Oolite.

Horizon and Localities. Marlstone, Spinatum Zone and Transition Bed, Tenuicostatum Zone ; Domerian to Whitbian Substages. It is reported from South Petherton and Ilminster, Somerset ; Stonehouse and Tuffley, Gloucestershire ; Adderbury and Cropredy, Oxfordshire ; Staverton, Northamptonshire ; Vale of Belvoir, Leicestershire ; Denton, Lincolnshire ; Staithes and Cleveland, Yorkshire.

Cardinia gigantea (Quenstedt 1856)

Plate 3, fig. 3

1856 *Thalassites giganteus* Quenstedt : 81, pl. 10, fig. 1.

Material. Several examples in the B.M.(N.H.) including the specimen here figured on Pl. 3, fig. 3. Dimensions of figured specimen : height 51 mm ; length 120 mm ; inflation 34 mm ; h/l = 42·5%.

Description. Concinnoid *Cardinia* with a more inflated shell, due to its relatively reduced height, than the taller and more flat-sided *C. concinna*. The flat postero-dorsal margin is almost parallel with the longitudinal axis and meets the evenly rounded, and posteriorly upswept, ventral margin in a tight curve. The anterior is more acutely rounded and slopes at a low angle and in a straight line from the small and depressed umbones. The lunule is fairly deeply excavated and the beaks slightly incurled. The shell surface is covered with irregular growth halts.

Comparisons. The upswept posterior of this species gives the shell a flattened and horizontal postero-dorsal outline and this, together with the small and pointedly projected anterior, distinguishes it from the round-backed, round-fronted, taller *C. concinna*.

Remarks. Quenstedt's original figured specimen came from the Lower Sinemurian of Gmuend, Germany. He recorded it from the Lower Lias in beds just below the occurrence of *Caenisites turneri* and above that of *Agassiceras scipionianum*. Concinnoids occur in Britain most commonly in the condensed Liassic deposits around the Radstock area in Somerset (usually only as internal moulds), in the Frodingham Ironstone of Lincolnshire, and in the Marlstone and Transition Bed. Those from Radstock and Frodingham are of Sinemurian age and stratigraphically earlier than those from the Marlstone and Transition Bed. Since these concinnoids are similar in shape, confusion by earlier authors has resulted in the apparent range of the stratigraphically higher *C. concinna* being extended down to include the specimens from the Sinemurian localities. The latter, being morphologically distinct, are therefore best assigned to Quenstedt's *C. gigantea* and the higher Domerian–Whitbian forms to Sowerby's *C. concinna*.

Horizon and Localities. Semicostatum–Obtusum Zones, Lower Sinemurian. Radstock, Somerset ; Scunthorpe, Lincolnshire ; Redcar, Yorkshire.

Cardinia lanceolata (Stutchbury 1842)

Plate 2, fig. 4

1842 *Pachyodon lanceolata* Stutchbury : 484 (text-figure).
1849 *Cardinia lanceolata* (Stutchbury) Brown : 213, pl. 88, figs 18, 19.

Material. Stutchbury's holotype, B.M.(N.H.) 47578, ex Bean Collection from the Lower Lias of Robin Hood's Bay, Yorkshire ; no other material seen. Dimensions : height 37 mm ; length 88 mm ; inflation 25 mm ; $h/l = 44\%$.

Description. Stutchbury described it 'shell lanceolate, anterior portion $\frac{1}{6}$ of the length, posterior portion acutely produced ; hinge line straight ; height 0·7, length 1·2, thickness 0·4'. This sole specimen has a straight postero-ventral margin which meets the evenly rounded venter in an acutely rounded posterior curve. The anterior is less sharply curved, passing into a shallow concavity in the anterior outline at the lightly excavated lunule. The moderately incurled beaks are situated on the anterior seventh of the length. A bluntly rounded umbonal ridge runs from the umbo to the sharply curved posterior, and the surfaces of the valves are covered

with irregular growth halts. The ventral edges of the valves are remarkably thickened and channelled, presenting the 'carinate–bisulcate' appearance of an arietitid ammonite. The hinge, not seen in the two-valved and articulated holotype, is probably similar to that of *C. gigantea*.

Both Stutchbury and Brown have depicted the shell as too short, and Agassiz has figured *C. attenuata* (1842–5 : pl. 12″, figs 1–3) under the name '*C. lanceolata*'.

Comparisons. *C. lanceolata* is similar to both *C. gigantea* and *C. attenuata* ; from the first it differs in being more sharply attenuated posteriorly, and from the second in being more bluntly acuminate anteriorly. *C. concinna* from the Domerian resembles this species but is more ovate in outline and not nearly so obviously 'pointed' posteriorly.

Discussion. Tate (in Tate & Blake 1876 : 389–390) mistakenly placed this species in synonymy with *C. concinna* and recorded both from the Bucklandi Zone (in Tate's sense this includes the Bucklandi–Turneri Zones of Dean, Donovan & Howarth 1961). Henderson (1934 : 550) recorded it from the Semicostatum Zone of Fretherne, Gloucestershire.

Horizon and Localities. Lower Sinemurian. Fretherne, Gloucestershire ; Robin Hood's Bay, Yorkshire.

Cardinia attenuata (Stutchbury 1842)

Plate 2, figs 5, 6

1842 *Pachyodon attenuatus* Stutchbury : pl. 10, figs 13, 14.
1843 *Cardinia lanceolata* (Stutchbury) Agassiz 224, pl. 12″, figs 1–3 (non Stutchbury).
1849 *Cardinia attenuata* (Stutchbury) Brown : 213, pl. 88, fig. 20.
1904 *Cardinia attenuata* (Stutchbury) Richardson : 220, pl. 15, fig. 10.

Material. Holotype in City Museum, Bristol, C 2156, and many others in that museum and also in the B.M.(N.H.). Dimensions of figured specimen, L 7020 : height 34 mm ; length 74 mm ; inflation 15 mm ; h/l = 46% (Pl. 2, fig. 6).

Description. 'Shell cuneiform ; transverse diameter twice its height ; posterior end strongly attenuated ; lunule small but deep ; transverse diameter 2·8, height 1·4, thickness 0·7' (Stutchbury 1842 : 485). The shell is ovately cuneiform with the dorsal and ventral margins converging posteriorly from the broadly rounded anterior, which terminates at a small lunule beneath slightly incurled and approximated beaks. The shell looks as if a typically elongated *C. ovalis* had become further 'stretched' out in a posterior direction so that the length is more than twice the height. The anterior has a broadly rounded curve, like a typical *C. ovalis*, which contrasts with the narrowly rounded posterior. The beaks are placed on the anterior quarter to fifth of the length, and are small and slightly projected. The hinge is lightly constructed, with small teeth as in *C. ovalis* and the rugoid group. Some examples are more cuneiform than others from the same bed owing to a relative reduction in the length. In the Raricostatum–Oxynotum Zones of Yorkshire and Raasay in Scotland an attenuated cardiniid occurs which is closely comparable in outline with the shortest examples of this species. These fall within the range of variation of the

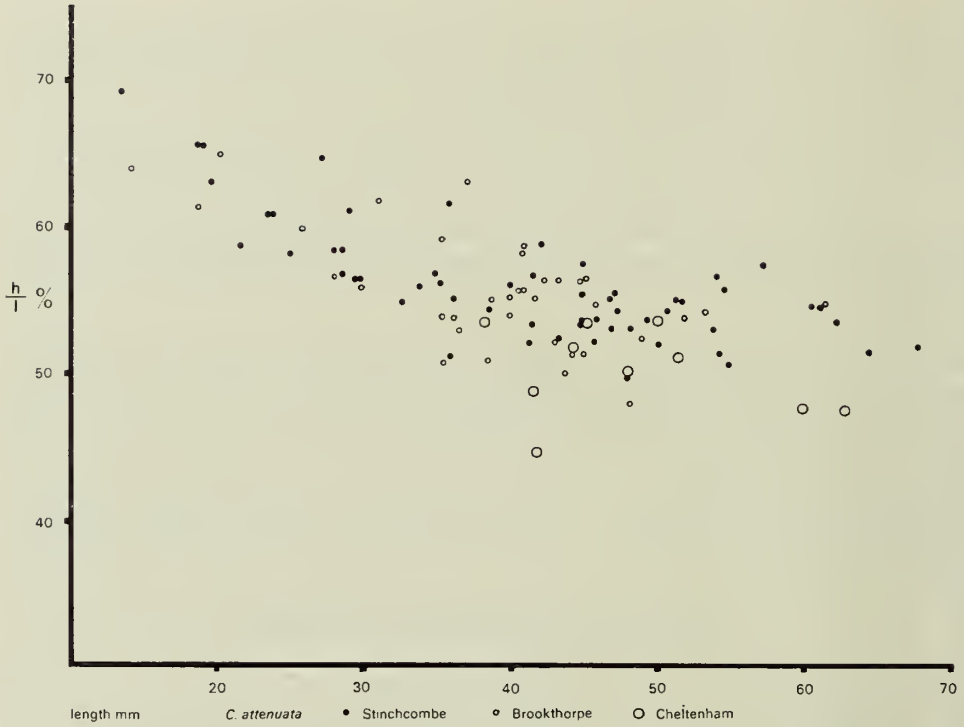

FIG. 8. *Cardinia attenuata* collected by Dr M. K. L. Curtis and Mr T. Fry from three localities in the Ibex Zone of Gloucestershire. The diagram demonstrates the reduction of the height : length ratio with increase in size.

stratigraphically higher Ibex Zone specimens of *C. attenuata* and are therefore here accepted as being conspecific.

COMPARISONS. Anterior to the beaks this is almost indistinguishable from the Hettangian *C. ovalis*, but the posterior portion is more extended and attenuated. It cannot be confused with *C. hybrida* since the beaks, as in *C. ovalis*, are set further back from the anterior margin. The anterior is more broadly rounded than in any of the other members of the concinnoid group.

REMARKS. Agassiz was misled by Stutchbury's poor sketch of *C. lanceolata* (1842 : 484) into believing that it was the same as *C. attenuata*. His figure of *C. lanceolata* (pl. 12″, figs 1–3) is based on a specimen from the Lias of Cheltenham, Gloucestershire, and there is no doubt that he has drawn a typical *C. attenuata*. A large collection of this species was made at several localities in the Ibex Zone of Gloucestershire. Fig. 8 shows the distribution of the height : length ratios and clearly demonstrates the increase of length with growth.

HORIZON AND LOCALITIES. Raricostatum Zone, Upper Sinemurian to Ibex Zone, Carixian Substage. It is reported from Cheltenham, Leckhampton, Battledown,

Mickleton, Stow Hill, Cam, Dumbleton, Stinchcombe, Brookthorpe, all in Gloucestershire ; Blockley clay pit, Worcestershire ; Napton and Little Wolford, Warwickshire ; Kilsby Tunnel and Kingsthorpe Shaft, Northamptonshire ; Husbands Bosworth, Leicestershire ; Robin Hood's Bay, Yorkshire ; Pabba Shales of Raasay, Scotland.

Cardinia tuffleyensis sp. nov.

Plate 4, figs 4–5

1882 *Cardinia hybrida* (Sowerby) Witchell : 107, pl. 2, fig. 4.

Specific name. From the village of Tuffley on the southern flanks of Robin's Wood Hill in Gloucestershire.

Material. Holotype a right valve only, B.M.(N.H.) LL 31275, from the Middle Lias, Margaritatus Zone, Bed 14, Tuffley, Robin's Wood Hill, Gloucestershire. Paratypes : one left valve from the same bed and locality as the holotype, and four single valves from the equivalent horizon, bed 10, at Stonehouse, Gloucestershire. Dimensions of holotype : height 31·2 mm ; length 74·4 mm ; inflation 8·0 mm ; h/l = 58% (Pl. 4, fig. 4).

Diagnosis. Concinnoid *Cardinia* resembling the young stages of the Marlstone forms of *C. concinna* but differing in its greater height : length ratio and flatter dorsal outline.

Description. Size small for a concinnoid *Cardinia*, ovately trigonal in outline, inequilateral, beaks situated at the anterior quarter of the length, inflation slight. Beaks pointed, prosogyrous, overhanging a deeply impressed lunule which, in the holotype, is bounded by a sharp ridge – paratypes do not exhibit this ridge. The anterior outline is slightly concave beneath the umbones and meets the regularly curving ventral margin in a bluntly rounded anterior projection. The distinct umbonal ridge descends steeply, nearly parallel with the dorsal margin, to the posterior edge, and growth lines and growth halts change direction sharply as they pass over the umbonal ridge. In the interior, the regular, but asymmetrical, arch of the hinge plate is interrupted by a ventrally directed fold at the posterior end of the deeply sunken nymph, and is terminated abruptly by the deeply set anterior and posterior adductor muscle scars. The left valve has the usual anterior socket and long posterior lateral. The right valve has an anterior peg-like lateral tooth and a long posterior socket.

Comparisons. This species closely resembles the equivalent growth stage of the much bigger, and stratigraphically higher, *C. concinna*, but it differs in its greater height : length ratio giving the shell a much taller appearance. Comparative h/l percentage ratios for the two species are : *C. concinna*, from the Marlstone, Spinatum Zone, 52%, 50%, 49% ; *C. tuffleyensis*, from the Margaritatus Zone, holotype 58%, paratypes 62%, 60%, 59%.

Horizon and Localities. Margaritatus Zone of the Domerian Substage. Bed 10 at Stonehouse Brick and Tile Co. Clay Pit, Gloucestershire ; Bed 14 at Tuffley Clay Pit, Robin's Wood Hill, Gloucestershire (Palmer 1972).

Cardinia rugulosa Tate 1875

Plate 5, fig. 5

1875 *Cardinia rugulosa* Tate : 508, text-fig. 3.

Material. Tate's original, which came from the Jamesoni Zone of Mungar quarry, Paulton, Somerset, cannot be traced in the Institute of Geological Sciences. However, B.M.(N.H.) L 77306, from the '*armatus* Zone' (Jamesoni Zone) of Bince's Lodge near Radstock, Somerset, is similar to Tate's sketch although slightly more sharply angled in its postero-dorsal outline. This specimen, a right valve, is here figured on Plate 5, fig. 5. No other material has been seen. Dimensions of figured B.M.(N.H.) specimen : height 9·5 mm ; length 15 mm ; inflation about 5 mm ; $h/l = 63{\cdot}5\%$.

Description. The sole specimen, a right valve, is small (15 mm long), and subquadrate in outline with the umbones on the anterior quarter of the length. The dorsal and ventral margins are nearly parallel, while the posterior slopes steeply from the sharp angle in the postero-dorsal margin. The beaks are small, and slightly incurled above a moderately excavated lunule. The surface is covered with about nine imbricating lamellae with upturned edges. The hinge, but poorly seen, is apparently similar to that of *C. ovalis* and *C. dayi*. Tate (1875 : 508) remarked of his specimen that the surface was 'ornamented with thick folds of growth, the umbonal ones with erect lamellose edges', and leaves no doubt that he was describing the same form as that figured here on Plate 5, fig. 5.

Comparisons. *C. rugulosa* is similar to *C. dayi* and *C. tutcheri*, and also to *C. toriyamai* Hayami (1958) from Japan, but it differs from all these in its squarer outline and more sharply angled postero-dorsal margin. This, together with its stratigraphically earlier occurrence, requires that it be treated as a distinct species.

Horizon and Locality. Jamesoni Zone, Carixian Substage of the Radstock area, Somerset.

Cardinia dayi sp. nov.

Plate 5, fig. 3

Specific name. After E. C. H. Day, who first described the Shell Bed in the Middle Lias of the Dorset Coast from which the type material was collected.

Material. Holotype, a left valve only, B.M.(N.H.) LL 31271. Paratypes : one right valve, B.M.(N.H.) LL 31272, and two left valves, LL 31273–4. All from Day's Shell Bed in the Middle Lias of the Dorset Coast ; all are broken. Dimensions of holotype : height 18·5 mm ; length 27·5 mm ; estimated inflation 9 mm ; $h/l = 65{\cdot}5\%$.

Diagnosis. Rugoid *Cardinia* resembling *C. torayamai* Hayami but differing from that species in its flatter ventral margin, more ovate outline and more deeply excavated lunule. From *C. rugulosa* it differs in its greater size and more ovate posterior outline.

DESCRIPTION. Size small for the genus, ovate, inequilateral, the beaks at about the anterior quarter of the length, inflation slight. Beaks slightly undercut at the antero-dorsal margin and strongly prosogyrous. Anterior margin (broken in holotype) sloping steeply from the subumbonal undercut and passing into a strong anterior curve which grades into the slightly convex outline of the ventral margin. A sharp curve at the postero-ventral margin passes into the smooth convexity of the postero-ventral outline, which is terminated at the anteriorly pointing beaks. Lunule small and bounded by a bluntly rounded ridge.

The exterior of the holotype has about fourteen concentric, flat, stepped lamellae which are slightly turned up at the edges and covered by fine growth lines. In the interior the slightly asymmetrical, but regularly arched, outline of the hinge plate is broken by a faint ventrally directed convexity below the nymph. The hinge plate is terminated at either end by the slightly impressed adductor muscle scars. Pallial line entire.

In the hinge the usual obsolescent cardinal 3b can barely be made out in the right valve, and the arrangement of the lateral teeth is typically cardiniid. The anterior part of the left valve contains a deep depression in the hinge plate for the reception of the peg-like protuberance at the end of the single anterior lateral tooth in the right valve. The posterior laterals of the right valve are formed by the dorsal margin (behind the nymph) beneath which a hollow is formed by a tooth which arches down from the hinge plate just behind the nymph, curves sharply, and rises to meet the hinge plate again just above the posterior adductor scar. The ventral outline of the hinge plate above this tooth is not altered by its presence and maintains a regular arching curve. A single posterior lateral in the left valve fits into the socket thus formed.

HORIZON AND LOCALITY. Lower Jurassic, Domerian, Margaritatus Zone Stokesi Subzone, Bed 20 of Howarth (1958), 'Day's Shell Bed', Seatown to Eype, Dorset coast.

Cardinia tutcheri sp. nov.

Plate 5, figs 1–2

SPECIFIC NAME. After J. W. Tutcher who collected the holotype.

MATERIAL. Holotype, B.M.(N.H.) 77369, a left valve from the Marlstone layer of the Junction Bed, Spinatum Zone, Thorncombe Beacon, Dorset ; J. W. Tutcher Collection. Paratype, B.M.(N.H.) 67374, a right valve only, which is badly eroded in the umbonal region, from the Middle Lias of Chideock, Dorset ; Etheridge Collection. In the paratype, the hard crystalline matrix enclosing ferruginous ooliths is identical with that of the holotype, so it also certainly came from the Marlstone layer (Spinatum Zone) of the Junction Bed. Dimensions of holotype : height 28·5 mm ; length 50·5 mm ; inflation 8 mm ; $h/l = 57\%$ (Pl. 5, fig. 1).

DIAGNOSIS. Rugoid *Cardinia* resembling *C. dayi* but differing in its reduced height : length ratio and more incurled beaks.

Description. Medium size (length of largest specimen, the paratype, is 56 mm), elongate and ovate in outline, inequilateral, beaks at about the anterior quarter of the length, inflation moderate.

Comparisons. This species strongly resembles *C. dayi* in all respects except in its greater relative length, slightly less prosogyrous beaks, and flatter ventral margin. The shell surface is composed of strongly imbricating flat lamellae upon which are fine growth lines. The hinge of neither specimen has been examined owing to the difficulty of developing the relatively soft shells from the hard crystalline matrix, but there are no reasons for supposing that the hinge differs much from that of *C. dayi* and *C. toriyamai*. However, the greater length of the shell implies that the hinge plate may be expected to form a flatter arch.

Horizon and Localities. Lower Jurassic, Domerian, Spinatum Zone, Marlstone layer of the Junction Bed. Seatown to Eype, Dorset coast.

V. EVOLUTION AND PALAEOECOLOGY

Evolution. Few exact statements may be made in this section because the establishment of a correct sequence of forms of *Cardinia* is entirely dependent on accurate zonal data accompanying the material to be studied. Unfortunately, this information is nearly always absent, even in the large accumulations of fossil bivalves constituting national collections. The stratigraphical assignments in Section IV are largely based on the author's field experience and deductions made from the literature. The former, though believed to be reliable, is always insufficient for our needs, while the latter, though abundant, is not always reliable. However, given that the horizons are more or less correct, the following tentative picture emerges.

The earliest British Jurassic forms are those occurring in the Hettangian Sutton Series of south Wales (a peculiar lithology consisting of white limestone with angular fragments of rock derived from the Carboniferous Limestone), a deltoid, *C. ingens*, and an ovoid, *C. suttonensis*. *C. ingens* has been seen in Liassic marginal facies around the Mendips and in Wurt Pit near East Harptree where it is associated with the ammonite *Psiloceras*. This deltoid is a strong candidate for the ancestor of *C. listeri* and *C. hybrida*, but no more so than the continental *C. angustiplexa* Chapuis & Dewalque or *C. dunkeri* Chapuis & Dewalque, both from the Hettangian Marne de Jamoigne of eastern France. However, the deltoids in Britain appear to have had a straightforward development through *C. listeri/hybrida* (Bucklandi–Semicostatum Zones), *C. raasayi* (Raricostatum Zone) to *C. idalia* (Spinatum Zone), and very probably to *C. slatteri* (Tenuicostatum Zone) since *C. idalia* is already, in the Spinatum Zone, developing a strong posterior carina and concave sides.

The ovoids probably developed from the doubtful *C. suttonensis* (Planorbis zone) to *C. ovalis* (Liasicus–Angulata Zones) and *C. crassiuscula* (Semicostatum–Obtusum Zones). It seems probable that *C. attenuata*, though grouped with the concinnoids on general shape, developed from one of the ovoids, rather than one of the concinnoids or one of the deltoids such as *C. hybrida*, since the ovoids have a rounded anterior margin and a tendency to elongate posteriorly (cf. *C. ovalis* var. *unioides*, p. 21) whereas *C. hybrida* has more prosogyrous beaks over a steeply sloping anterior.

The origin of the concinnoids is obscure but it seems probable that they evolved from one of the ovoid stock. Having done so somewhere in the Sinemurian they subsequently maintained themselves as a tight group from *C. lanceolata* (Bucklandi–Turneri Zones), to *C. gigantea* (Semicostatum–Obtusum Zones) and *C. concinna* (Margaritatus–Tenuicostatum Zones).

In the rugoids it is easier to demonstrate a stratigraphical sequence because there are fewer examples, and these are from well-documented horizons ; the trends shown by them seem to be straightforward. A specimen of *Cardinia* sp. in the B.M.(N.H.) (66216, purchased from M. Tesson in 1896 ; Pl. 5, fig. 4) is recorded from the 'Upper Lias' of France. No other information is available, but the French origin is not in doubt since it is registered next to one lot of *C. gibbosula* d'Orbigny (= *C. itea* d'Orbigny) from the 'Upper Lias of Fontaine Etoupefour, France', the preservation of which is identical with that of specimen no. 66216. The surface sculpture and shape closely resemble those of *C. tutcheri* from the Marlstone of Dorset but it is more depressed and, in this character, it continues the trend seen in the earlier rugoids, and provides a terminal form to an interesting stratigraphical sequence. This starts with the small square *C. rugulosa* and is continued with the larger and more ovate *C. dayi* which, by depression of the dorsal margin and elongation, leads to *C. tutcheri* and finally to the un-named French form exemplified by B.M.(N.H.) 66216.

The height : length ratios of these forms, at 15 mm height, are as follows :

Species	Horizon	Locality	*h/l* (%)
Cardinia sp.	Toarcian	France	50
C. tutcheri	Spinatum Zone	Dorset	57
C. dayi	Margaritatus Zone	Dorset	66
C. rugulosa	Jamesoni Zone	Somerset	63·5

No difference in the character of the hinge is detectable between the earliest and latest cardiniids. The functional anterior and posterior laterals remain constant both in position and size and, apart from slight individual variations, they do not alter. The sole obsolescent cardinal tooth 3b in the right valve can usually be detected as a more or less elongated rounded ridge. Examination of a number of hinges shows a tendency for this tooth to be most strongly developed in deltoids, and weakest in ovoids, but it is never sufficiently developed to be regarded as functional.

Beyond the Transition Bed (Tenuicostatum Zone) there are no reliable records of *Cardinia* in Britain and it seems, from the available evidence, that the genus became extinct at this horizon in Britain and later, during Whitbian times, throughout Europe.

Palaeoecology. Cardiniids are found in almost every kind of Liassic lithology ; shales, limestones, sandstones, ferruginous oolitic limestones but not in paper shales. It does not seem possible to relate any of the infrageneric groups to a particular lithology, except that the author has not seen a concinnoid from a shale or muddy deposit.

The associates of *Cardinia* are many, varied and almost always molluscs ; and of these, considered singly, only *Astarte* has been found to be a frequent associate. At

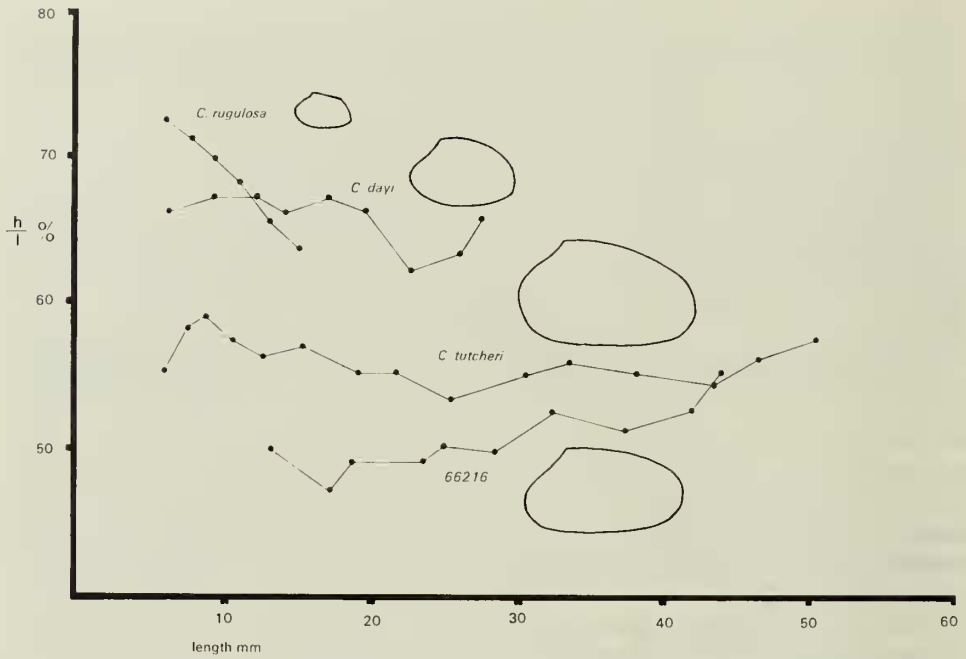

FIG. 9. A stratigraphical sequence of British rugoid cardiniids; oldest at the top, youngest at bottom. The diagram represent height : length ratios in *Cardinia rugulosa*, Jamesoni Zone ; *C. dayi*, Margaritatus Zone ; *C. tutcheri*, Spinatum Zone ; and the French specimen, B.M.(N.H.) 66216, from the Whitbian Substage at Fontaine Etoupefour. The tendency towards elongation in the development of *C. rugulosa*, and also in the sequence of *C. dayi*, *C. tutcheri* and specimen 66216, is well demonstrated by this diagram. The possibility that this might in fact be an evolutionary sequence cannot be overlooked. Measurements were made on single valves of each of the species at various growth stages and outlines drawn as left valves for uniformity.

Kilve in north Somerset *C. ovalis* is found in Hettangian shales and is there accompanied by *Astarte obsoleta* Dunker, in the proportion of 10–15 *Cardinia* to 1 *Astarte*. The only other associates, apart from ammonites, are rare oysters and even rarer scaphopods. The same two species are also found in Hettangian shales at Evesham, Worcestershire, where the ratio is about 15–20 *Cardinia* to 1 *Astarte*, but there the association is masked by the presence of other bivalve molluscs, particularly *Liostrea irregularis* (Münster). At a higher horizon in the Frodingham Ironstone of Lincolnshire, *Cardinia* and *Astarte* also occur together, but there the *Astarte* is rare, and the estimated ratio is about 50–100 *Cardinia* to 1 *Astarte*.

The richly fossiliferous shell beds seen at Blockley, Worcestershire, and around Cheltenham and Gloucester, Gloucestershire, are in the Ibex Zone. In Gloucestershire both *Astarte* and *C. attenuata* are abundant in the Valdani Subzone, but in the slightly later (Luridum Subzone) shell bed at Blockley Station *Astarte platymorpha* Cossman (Palmer 1973 : 260) dominates to the exclusion of *C. attenuata* which does, however, occur in the clays below, somewhat rarely and without *Astarte*. This

apparent 'trend' is negated in the Margaritatus Zone of Gloucestershire and Dorsetshire, for there the two are again associated. In Gloucestershire they are about equally rare, and in Dorsetshire *Astarte* dominates about 15 : 1.

It is difficult to offer convincing reasons why these two genera should exhibit such an erratic relationship, and one is tempted to speculate on possible physio-chemical factors of the benthonic environment, and isostatic movements of the seafloor, when possibly the relative abundance of the two genera was controlled simply by the distribution of their larvae in the plankton. The ecological factor which controlled the absolute distribution of *Cardinia*, that is whether they are present or not, is no easier to discover, for clearly sediment grade played little or no part. The hypothesis that they were controlled by the availability of dissolved oxygen is a little devious and admittedly tenuous, but it is perhaps worth expounding.

Of the many factors controlling the distribution of bivalve molluscs the essential three are a suitable substrate for the settlement of spat, and the availability of food and dissolved oxygen. In *Cardinia* the shell-shape and absence of a pallial sinus indicate that they were shallow burrowers ; while the strong shear-resistant lateral teeth forming the hinge indicate that they were also active animals. Active, shallow-burrowing, filter-feeding bivalves need suspended organic debris, and oxygen to 'drive' the filtering gill.

Cardiniids are often associated, among other things, with small holostomatous gastropods belonging to the Trochacae. It has already been shown that the presence of trochid gastropods has some depth implications (Palmer 1973 : 261), since almost all living trochids are algal grazers and are therefore necessarily confined to the 'photic zone' which, for the purpose of this argument, is best extended down to its lowest limit of about 100 m. The two *Cardinia* beds in the Frodingham Ironstone contain an ovoid *C. crassiuscula* and a concinnoid *C. gigantea* in the ratio of 10–20 to 1. Their abundance in the ironstone contrasts with their virtual absence from the shales above which, at Roxby, extends to the Upper Lias. The inhibiting factor is not easy to discover since ovoids are present, and abundant, in the shales at Evesham but there they are associated with a small trochid gastropod in the lower of the two *Cardinia* beds. In the shales above this bed both the *Cardinia* and the trochid are absent, or so rare as to have escaped the attention of three careful searchers ; the *Cardinia* does not return until the Upper *Cardinia* bed, some 6 m higher in the succession, where it is accompanied by abundant oysters and *Modiolus* but apparently without the gastropod.

The presence of the trochids in the silty sediments of the Lower *Cardinia* bed at Evesham strongly suggests that it was deposited within 100 m depth, and their absence from the finer shales above suggests a depth below 100 m. Deepening of the water below 100 m may have deprived the algal-grazing trochids of their food, but not the filter-feeding cardiniids since the presence of *Plagiostoma* in the shales above the Lower *Cardinia* bed proves that food was available. The evidence at Kilve and Blockley shows that fine shales are a suitable substrate for the settlement of *Cardinia* spat. It is therefore concluded that oxygen availability was the controlling factor in the distribution of *Cardinia* in the Hettangian shales at Evesham and very probably wherever it occurs. Deepening of the Liassic sea, as indicated by a change to

finer sediments, could not by itself have affected the distribution of *Cardinia*. Only when this was accompanied by a significant drop in the dissolved oxygen content were the active, filter-feeding *Cardinia* unable to feed – even when food was available.

The life position of *Cardinia* may be tentatively inferred from the following observations. Two B.M.(N.H.) specimens show borings of other organisms (? sponges) along the postero-dorsal margin. The first is the holotype of *C. concinna*, see Pl. 3, figs 1, 2 ; the second is B.M.(N.H.) 43219, the *C. crassiuscula* derived into the Red Crag (p. 20). The borings are shallow circular holes occupying such a position as to indicate that the shells lay partially buried in sediment with their long axes inclined up to about 60 degrees from the horizontal, and possibly with the posterior part of the shell just protruding above the surface of the sediment. But since the majority of cardiniids show no signs of boring or encrusting organisms it seems probable that they were for the most part entirely buried in the sediment while alive. Only occasionally were dead shells exposed as a result of erosion, and these, which were almost certainly in the life position if undisturbed by bioturbation, were then available for boring organisms to attack.

VI. GENERIC RELATIONS

The taxonomic history of *Cardinia* was thoroughly reviewed by Cox (1961) and for the present purposes the following summary will suffice. In 1817 J. Sowerby described four new fossil shells which he named *crassissimus*, *listeri*, *hybridus* and *crassiusculus* ; he referred these shells with confidence to the fresh-water genus *Unio* and in doing so remarked with some astonishment that Mr Parkinson '– has, not without doubting, made it a *Donax*'. The subsequent recognition that these typically Liassic shells constituted a distinct genus from *Unio* resulted in the rapid proposal of the names *Thalassides* Berger 1833, *Ginorga* Gray 1840 (nom. nud.), *Cardinia* Agassiz 1841, *Sinemuria* de Christol 1841, *Pachyodon* Stutchbury 1842, and much later *Storthodon* Zittel 1881. Opinion 292 (1954) of the International Commission on Zoological Nomenclature validated the name *Cardinia* dating from Agassiz 1841 with *Unio listeri* J. Sowerby as type species, and suppressed *Thalassides* Berger and *Sinemuria* de Christol. Hayami (1958 : 21) unfortunately cited *Unio concinnus* as type species after the publication of Opinion 292 in which *Unio listeri* J. Sowerby was declared the type species.

The history of the systematic positioning of the genus is one which reflects the confusion resulting from a shell with the superficial appearance of a unionid but with an undoubted heterodont hinge. Agassiz (1843) placed it near the Unionidae, while Woodward (1854) placed it near the 'Cyprinidae' (i.e. Arcticidae). Chenu (1862) thought it was a crassatellid, while Stoliczka (1871) placed it in the Astartidae. Zittel (1881 : 61) proposed the family Cardiniidae which included not only *Cardinia* but several non-heterodont genera which are now referred to the Anthracosiidae and Pachycardiidae. Fischer (1887) placed Zittel's family Cardiniidae just before the Carditidae and only two families subsequent to the Unionidae – a fine compromise. Subsequent authors, who included Neumayr, Waagen, Dall, Deschaseaux and Cox,

expressed opinions that oscillated between relating the Cardiniidae either to the Unionidae or to one of the two heterodont families Astartidae and 'Cyprinidae' (Arcticidae). The present position of the genus, and a more rationally composed family Cardiniidae, in the *Treatise on Invertebrate Paleontology* (Cox 1969 : N578) is in the Crassatellacae next to the Crassatellidae. While supporting the inclusion of the Cardiniidae in the Heterodonta its position in the Crassatellacae is here challenged, and arguments in support of placing the genus *Cardinia* and the family Cardiniidae in the Lucinacae are offered below.

Cox (1961 : 328) remarked that 'forms with cardiniid dentition show a very similar range in external morphology to forms with astartid dentition'. He continued by citing three examples :

(1) the Triassic genus *Torastarte*, originally referred by its author Marwick (1953 : 70) to the Astartidae, but subsequently shown to be a cardiniid by Fleming (1957) ;
(2) the young of *Cardinia laevis*, frequently misidentified and recorded as *Astarte striatosulcata* Roemer ;
(3) the close similarity of the remarkable *Cardinia slatteri* Wilson & Crick to the astartid genus *Opis*.

These are strong arguments in support of his position and he might have continued to show the parallel development in shape of *Cardinia concinna* (J. Sowerby) and *Coelastarte excavata* (J. Sowerby) ; of *Cardinia listeri* (J. Sowerby) and the astartid *Bythiamena isosceles* Gardner ; of *Cardinia ovalis* (Stutchbury) and *Astarte dentilabrum* Etheridge ; and of *Cardinia quadrata* Agassiz and the three rhomboid astartids *A. platymorpha* Cossmann, *A. camertonensis* Moore and *A. rhombea* Roemer. But perhaps Cox was not altogether convinced, since none knew better than he that little significance can be attached to similarities in general morphology in support of postulated relationships when, as in this case, the really significant factor, the hinge, clearly showed that cardiniids and astartids are not closely related.

The dentition of an astartid is typically composed of two strong cardinals in each valve with laterals either absent or but weakly developed. There are departures from this pattern but they are not typical. On the other hand *Cardinia* constantly has strong laterals which, unlike the astartid lamellar teeth, tend to be tubercular. The cardinals are always weak or absent and it is difficult to recognize more than the single tooth 3b in the right valve.

Two examples can now be cited that should counter Cox's citation of *Torastarte* (which looks like an astartid but has a cardiniid dentition), as evidence of astartid affinities. They also show that the relationship of *Cardinia* is more likely to be with the Lucinacae.

(1) Cossmann (1904 : 521, pl. 17, figs 28, 29) published figures of a remarkable ovoid cardiniid, from the Hettangian (Infralias) of La Vendée, France, which he called *Cardinia lucinaeformis*, and which looks like a *Lucina* but has the hinge of a *Cardinia*. This fact would have clearly no more significance than a bivalve which has the appearance of an astartid and the hinge of a cardiniid (Cox's argument) were it not for the remarkable similarity that the hinge of the small Sinemurian lucinoid

bivalve '*Lucina*' *limbata* Terquem & Piette has to that of a typical cardiniid. Pl. 5 fig. 11 demonstrates in *Lucina limbata* the obsolete *Cardinia*-like cardinal teeth and the anterior lateral AII and AIV forming a socket for the reception of AIII in the right valve. Strong posterior laterals in the left valve make a socket for the reception of the tooth PIII in the right valve. The rest of the hinge with its weak cardinal 3b and strong laterals is very similar in general appearance to the hinge of *Cardinia*.

(2) Further evidence, demonstrating a greater affinity of *Cardinia* with lucinids than with astartids, includes :

(i) The external shell surface of *Cardinia* is made up of concentric, imbricating lamellae, sometimes with upturned edges as in the rugoids *C. dayi*, *C. rugulosa*, *C. tutcheri* and *C. toriyamai*. A similar kind of shell surface is found in many lucinids, but astartids generally have concentric undulations, almost never with imbricating lamellae.

(ii) In *Cardinia* the concentric ornament during ontogeny tends to get stronger whereas in astartids there is a tendency for concentric ornament to weaken.

(iii) The margin of *Cardinia* is always smooth while astartids usually have a denticulate ventral margin to the shell.

(iv) The ligament is clearly visible and external in astartids, making a prominent arch behind the umbones. In *Cardinia* it is deeply sunk within a narrowly lanceolate escutcheon. The condition of a deeply set ligament in the Lucinacae is common.

VII. CONCLUSIONS

The genus *Cardinia* is probably more closely related to Lucinacae than to Crassatellacae and the same is very probably true of the family Cardiniidae, as now constituted. The origins of the genus remain obscure but the Triassic genus *Torastarte* with its *Cardinia*-like hinge, similar external appearance and deeply sunk ligamental nymph is an obvious candidate. The extinction in Europe of *Cardinia* in the Whitbian Substage of the Toarcian Stage seems to coincide with the widespread transgression and change of fauna and lithology at that level. Little is known of the ecology of *Cardinia* except that they were clearly active, shallow burrowers in many kinds of sediments and, since they were bigger and more numerous in high energy environments and are seldom, if ever, found in paper shales, it is suggested that availability of oxygen rather than of food was the controlling factor in their distribution.

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IX. INDEX

New taxonomic names and the page numbers of the principal references are printed in **bold** type. An asterisk (*) denotes a figure.

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